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# ENDOHELMINTHS OF A SNAKE MACKEREL, *GEMPYLUS SERPENS* (TRICHIUROIDEA: GEMPYLIDAE), FROM THE GULF OF MEXICO

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**ABSTRACT:** Endohelminths are reported from a female snake mackerel, *Gempylus serpens* (Trichiuroidea: Gempylidae), captured from a depth of 61 m in the Gulf of Mexico 140 km south of the mouth of Mobile Bay, AL, in August 1998. A diverse endohelminth parasite fauna was found: 29 plerocercoid type I tetraphyllideans from the lower intestine; 4 didymozoid metacercariae allocated to the collective group *Monilicaecum* and one didymozoid metacercaria of the collective group *Torticaecum* from the pyloric cecum; one juvenile *Gonocerca phycidis* from the stomach; and 5 larvae (L3 stage) comprising 3 species of *Anisakis* from the pyloric cecum. These nematodes were identified as species of *Anisakis* due to the presence of an oblong ventriculus lacking an appendix, no intestinal cecum or interlabia, 3 lips with dentigerous ridges, and an excretory pore located between the lateroventral lips. Differences in overall size and in the lengths of the ventriculus and esophagus in relation to total body length were used to distinguish the 3 species of *Anisakis* collected. Seven specimens of a possibly unnamed species of parasitic copepod representing *Bomolochus* infected the gill chamber. Stomach contents included 6 early-juvenile flatfish (Pleuronectiformes). All of the helminths are measured and illustrated, and for some of the parasites recovered, we are unaware of any reports from this host species.

## INTRODUCTION

The snake mackerel, *Gempylus serpens* Cuvier (Trichiuroidea: Gempylidae), is the sole member of *Gempylus* Cuvier, representing one of 16 genera within Gempylidae (Nakamura and Parin 1993, Nelson 2006, Froese and Pauly 2009). Like many gempylids, *G. serpens* reportedly is a cosmopolitan, solitary, meso- or bathypelagic fish that ranges in tropical and subtropical seas to 600 m (Nakamura 1990, Nakamura and Parin 1993, Froese and Pauly 2009). *Gempylus serpens* exhibits diel vertical migration and feeds on fishes (myctophids, exocoetids, sauries, scombrids), squids, and crustaceans (Nakamura and Parin 1993). The species sporadically appears as bycatch in the tuna longline fishery, but there is reportedly no directed fishery for *G. serpens* (Nakamura and Parin 1993).

Prior to this study, only 5 parasite species have been reported from *G. serpens* (Table 1). As *G. serpens* is neither sought after nor kept by fishermen and there are no reports of parasites of *G. serpens* from the Gulf of Mexico, the purpose of this study was to survey the parasites of a snake mackerel captured in the Gulf of Mexico.

## MATERIALS AND METHODS

A mature female *G. serpens* was obtained at a fishing tournament in Destin, FL, and examined for metazoan parasites. The fish was captured 1 August 1998 from 140 km south of Mobile Bay, AL, (29°00'N, 87°50'W; time of capture = 0400 h; depth of fish = 61 m; total length = 78.5 cm;

weight = 452.6 g) and placed on ice for 2 days until necropsy and removal of parasites in the laboratory. While fixation of worms *in situ* is not ideal, we found that the quality of the specimens was good and features of taxonomic importance could easily be identified. Platyhelminths were stained in Van Cleave's hematoxylin, dehydrated in a graded ethanol (EtOH) series, cleared in clove oil, and mounted in Canada balsam. Nematodes were cleared in a solution of 5 parts glycerin with 95 parts 70% EtOH, and mounted in glycerin jelly. Copepods were placed in 70% EtOH. Drawings were made with the aid of a drawing tube. Measurements are in micrometers (µm), except where indicated in the text, and the mean followed by range and number of measurements (n) follow in parentheses where appropriate. Identification of the fish was based on Nakamura and Parin (1993) and fish systematics and taxonomic authorities follow FishBase 2009 (Froese and Pauly 2009). Endohelminths were deposited in the Harold W. Manter Laboratory of Parasitology (HWML), University of Nebraska-Lincoln, Lincoln, NE, USA.

## RESULTS AND DISCUSSION

We observed 6 early juvenile flatfish (Pleuronectiformes) in the stomach of the snake mackerel; 4 partially digested with lengths of 1.8 cm, 1.9 cm, 2.2 cm, and 2.8 cm and 2 almost completely digested with lengths of 1.8 cm and 2.0 cm, respectively. Small pieces of unidentifiable debris and tissue, including 1 vertebra, were also removed from the stomach.

**TABLE 1.** Records of parasites from the snake mackerel, *Gempylus serpens* Cuvier, 1829.

Parasite	Infection Site	Locality	References
Cestoda			
Plerocercoid type I tetraphyllideans	Lower intestine	Northern Gulf of Mexico	Present study
Digenea			
Didymozoid metacercaria type I [collective group type <i>Monilicaecum</i> ]	Pyloric cecum	Northern Gulf of Mexico	Present study
Didymozoid metacercaria type II [collective group type <i>Torticaecum</i> ]	Pyloric cecum	Northern Gulf of Mexico	Present study
<i>Dinurus barbatus</i> (Cohn, 1902)	Stomach	Indian Ocean, SW Pacific Ocean off NW Australia	Korotaeva and Koryakovtseva 1983
<i>Gonocerca phycidis</i> Manter, 1925 juvenile	Stomach	Northern Gulf of Mexico	Present study
Acanthocephala			
<i>Bolbosoma heteracanthae</i> larvae (Heitz, 1920)	Body cavity & internal organs	E & W Equatorial Pacific Ocean	Kovalenko 1981, Klimpel et al. 2001
<i>Gorgorhynchus robertdolfusi</i> Golvan 1956	Small intestine	Port-Etienne, Mauritania	Golvan 1956, Yamaguti 1963a, Golvan and Houin 1964, Kovalenko 1981, Vassiliadès 1985
Nematoda			
<i>Anisakis</i> larvae type I	Body cavity & internal organs	Philippine Sea	Bagrov 1982
<i>Anisakis</i> sp. 1, 2, 3	Mesenteries, pyloric cecum	Northern Gulf of Mexico	Present study
Copepoda			
<i>Bomolochus</i> sp.	Gill chamber	Northern Gulf of Mexico	Present study
<i>Sarcotretes gempyli</i> (Horst, 1878)	Penetrating outer body wall	Unknown*	Horst 1878, Wilson 1917, Yamaguti 1963b

\*Hosts were museum-stored specimens lacking locality data.

Helminths found included 29 plerocercoid type I tetraphyllideans from the lower intestine, 4 didymozoid metacercariae type I and one didymozoid metacercaria type II from the pyloric cecum, one juvenile *Gonocerca phycidis* Manter, 1925 (Digenea: Derogenidae) from the stomach, and 5 larvae (L3 stage) comprising 3 species of *Anisakis* Dujardin, 1845 (Nematoda: Ascaridoidea) from the pyloric cecum. Seven specimens of a seemingly unnamed species of *Bomolochus* von Nordmann, 1832 (Poecilostomatoida: Bomolochidae) infected the gill chamber and will be detailed in a separate paper (G. Benz, personal communication).

#### Descriptions of Species

##### CESTODA

##### ORDER TETRAPHYLLIDEA CARUS, 1863

##### PLEROCERCOID TYPE I (Figure 1A)

**Description:** Based on 23 specimens. Small subglobular to

conical plerocercoids, no visible segmentation. Length 218 (161–300; n = 21); width at midbody 59 (49–72; n = 21). Scolex with 4 subspherical, undivided bothridia; simple apical sucker. Scolex length from posterior edge of bothridia to anterior tip 59 (49–74; n = 22); width at level of widest point along scolex length 71 (62–85; n = 21). Bothridia 36 (29–47; n = 88) long, 28 (17–43; n = 88) wide. Apical sucker 32 (27–55; n = 22) long, 41 (37–50; n = 22) wide.

**Site of infection:** Lower intestine.

**Deposited specimens:** HWML voucher 49132 (6 slides).

**Remarks:** The collective group name *Scolex pleuronectis* Müller, 1780 (and *Scolex polymorphus* Rudolphi, 1819) is assigned for unidentifiable larvae as is generally accepted when describing tetraphyllidean plerocercoids for which the adult form is unknown (Overstreet 1978). These unidentified larvae labeled by the collective group name *S. pleuronectis* have

been reported from many localities world-wide and infect the intestine of many marine teleosts before maturing in the gut of elasmobranchs. Probably because the collective group *S. pleuronectis* includes many species, these larvae vary in size and shape (Caira and Reyda 2005).

When compared with larval cestodes reported by Dollfus (1964), these specimens appear superficially similar to *Scolex polymorphus unilocularis* Olsson, 1869 reported from the cuttlefish *Sepia officinalis* Linnaeus in overall appearance including 4 sessile, undivided, spherical bothridia and a single apical sucker. These specimens also bear resemblance to the tetraphyllidean metacestode identified by Chambers et al. (2000) as type 4 metacestode, obtained from 12 families of teleosts collected along the Great Barrier Reef, in having a

conical shape, a single apical sucker and 4 simple unilocular bothridia.

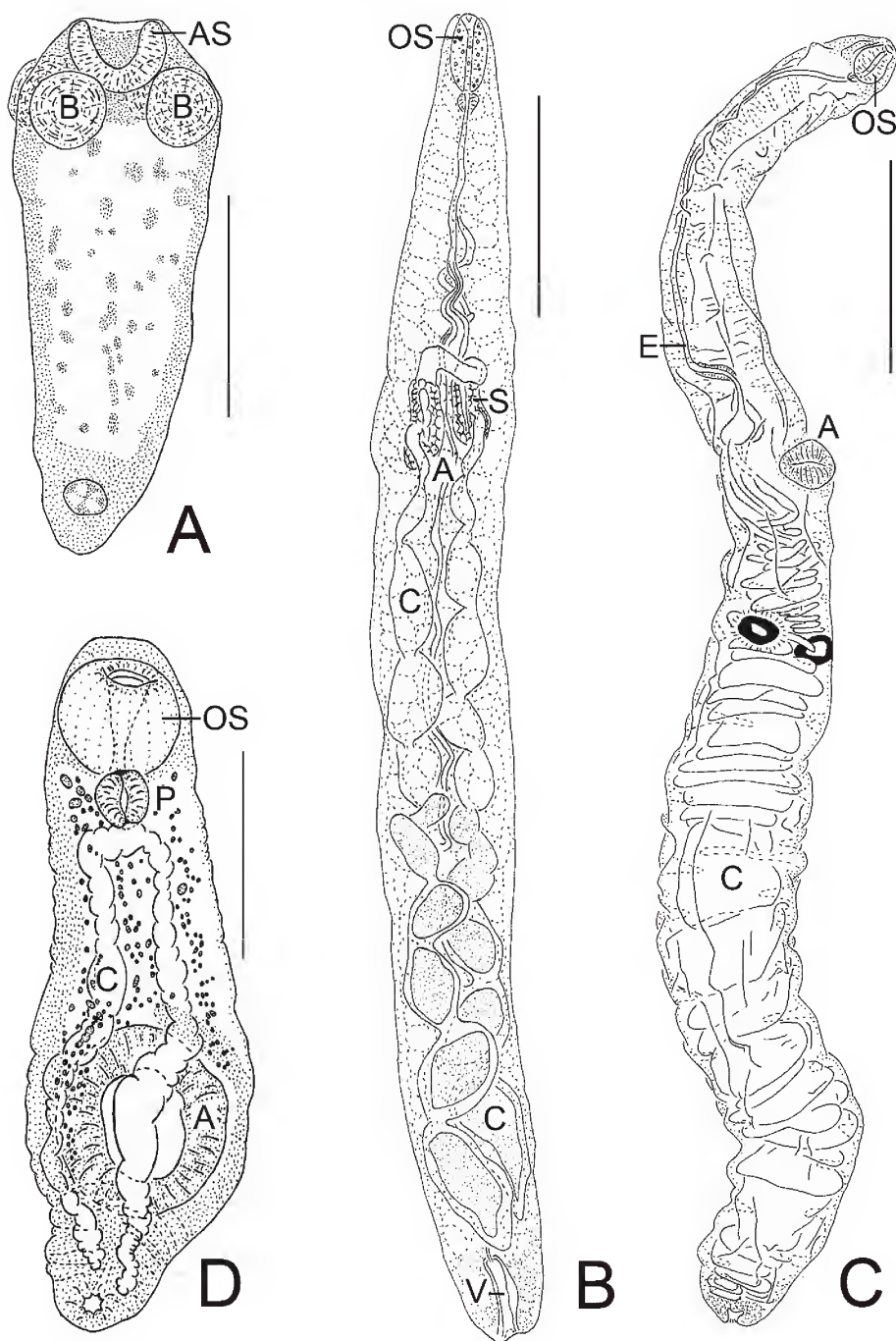
The valid collective group name *Scolex pleuronectis* represents an indeterminate number of species, the life cycles of none of which have been elucidated or studied in any great detail. Therefore, we caution against presenting a collective group name as comprising a new host record because it does not represent a species; however, we are unaware of any prior report of a cestode from *G. serpens*.

#### DIGenea

#### FAMILY DIDYMOZOIDAE MONTICELLI, 1888

#### DIDYMOZOID METACERCARIA TYPE I (Figure 1B)

*Description:* Based on 4 specimens; 2 intact, 2 damaged. Unencysted. Body elongate, dorso-ventrally flat, with



**Figure 1.** Illustrations of cestode and digenean parasites from *Gempylus serpens*.

A. Plerocercoid type I, entire, lateral view. Scale bar 100 µm.

B. Didymozoid metacercaria type I, entire, dorsal view. Scale bar 300 µm.

C. Didymozoid metacercaria type II, entire, dorsolateral view; note 2 thick black rings denoting holes at midbody where specimen was damaged. Scale bar 3.475 mm.

D. Juvenile of *Gonocerca phycidis*, entire, dorsal view. Scale bar 1 mm.

Abbreviations: A, acetabulum; AS, apical sucker; B, bothridium; C, cecum; E, esophagus; OS, oral sucker; P, pharynx; S, stomach; V, excretory vesicle.



bluntly-rounded to truncated ends, 1,817 (1,575–2,211;  $n = 3$ ) long, 87 (74–104;  $n = 3$ ) wide at level of pharynx, 185 (169–229;  $n = 4$ ) wide at level of acetabulum, and 123 (99–140;  $n = 4$ ) wide at level of distal ends of ceca. Forebody tapering to round or truncate anterior extremity, 598 (516–721;  $n = 3$ ) long, 124 (109–135;  $n = 3$ ) wide at level of midpoint of forebody; 32 (32.6–33.4%;  $n = 3$ ) of body length. Hindbody of uniform width, round at posterior extremity, 1,226 (1,058–1,491;  $n = 4$ ) long. Tegument smooth. Body filled with vesicular parenchyma. No eyespots or eye pigment observed. Oral sucker oval to panduriform, sometimes protruding, 105 (96–112;  $n = 3$ ) long, 55 (52–62;  $n = 3$ ) wide, composed of outer longitudinal muscles and inner circular muscles; large vesicular transparent cells throughout interior of sucker; mouth terminal. Acetabulum muscular, sessile, subspherical, small, 65 (59–72;  $n = 4$ ) long, 68 (62–72;  $n = 4$ ) wide, pre-equatorial along longitudinal axis near junction of anterior and middle thirds of body. Oral sucker to acetabulum length ratio, 1:0.6 (1:0.6–0.7;  $n = 3$ ); oral sucker to acetabulum width ratio, 1:1.2 (1:1.1–1.4;  $n = 3$ ). Distance between suckers, 498 (422–622;  $n = 3$ ); ratio of distance between suckers to body length, 1:3.7 (1:3.6–3.7;  $n = 3$ ). Prepharynx not observed. Pharynx spherical, 28 (24–32;  $n = 3$ ) long, 28 (27–33;  $n = 3$ ) wide. Esophagus long, 364 (312–454;  $n = 3$ ) long, 13 (7–23;  $n = 3$ ) wide at midpoint; either thin-walled anteriorly becoming more thick-walled and sinuous posteriorly or entirely thick-walled; thickness of esophageal wall at posterior end, 8 (7–10;  $n = 2$ ) wide. Cecal bifurcation preacetabular, forming thick-walled ‘Drüsenmagen’ (= stomach) lined with glandular cells, extending anteriorly from acetabular level to region immediately preacetabular, 212 (146–261;  $n = 4$ ) long, 89 (84–92;  $n = 4$ ) wide at anterior end and 115 (79–149;  $n = 4$ ) wide at posterior end. Ceca wide, descending in undulating moniliform fashion, consisting of series of smooth, thin-walled, inflated chambers filled with fluid that is clear to tan in smaller, anterior chambers, becoming darker in larger, more-developed posterior chambers. Total number of cecal chambers, 22–24; number of chambers per cecum, 11–12. Anterior cecal chamber smallest, 65 (47–105;  $n = 8$ ) long, 24 (12–38;  $n = 8$ ) wide; middle cecal chamber intermediate in size, 82 (71–107;  $n = 8$ ) long, 72 (52–105;  $n = 8$ ) wide; posterior cecal chamber largest, 234 (181–305;  $n = 8$ ) long, 94 (71–132;  $n = 8$ ) wide. Ceca ending blindly, 99 (89–114;  $n = 4$ ) long from posterior end of body. Genital anlagen not observed. Excretory vesicle I-shaped, posterior portion sac-like, 97 (89–110;  $n = 4$ ) long, 25 (9–50;  $n = 4$ ) wide, narrowing into long, thin tube running anteriorly up to about midpoint of forebody; bifurcation of excretory vesicle not confirmed. Numerous numbers of parenchymal cells around excretory vesicle and posterior end of worm. Excretory pore terminal.

*Site of infection:* Pyloric cecum.

*Deposited specimens:* HWML voucher 49133 (2 slides).

*Remarks:* These didymozoid metacercariae belong to the collective group type *Monilicaecum* in that they possess a stomach and acetabulum as well as ceca with moniliform chambers or conspicuous swellings. *Monilicaecum*, first given generic status by Yamaguti (1942), is now regarded as a collective larval group name for the first free didymozoid juvenile stages that form in fish hosts (Yamaguti 1970, 1971). These specimens also appear similar to members within the collective group *Paramonilicaecum* Kurochkin and Nikolaeva, 1978 in possessing an acetabulum, pharynx and stomach yet lacking gland cells around the distal region of the esophagus, stomach and/or ceca (see Pozdnyakov and Gibson 2008).

As stated earlier, we caution against presenting a collective group name as comprising a new host record because it does not represent a valid species; however, we are unaware of a prior report of a didymozoid from *G. serpens*.

DIDYMOZOID METACERCARIA TYPE II (Figure 1C)

*Description:* Based on one contracted and damaged specimen. Unencysted. Body elongate, flattened dorso-ventrally, with bluntly-rounded ends, 3,345 long, 159 wide at level of pharynx, 258 wide at level of acetabulum, and 194 wide at level of distal end of ceca. Forebody long, equal in width, 1,218 long or 36% of body length, 169 wide at level of midpoint, with rounded anterior extremity. Hindbody length 2,127 long, about equal to 2/3 of body length, widest at level of junction of middle and posterior thirds of body, with rounded posterior extremity. Tegument smooth. Body filled with vesicular parenchyma; parenchymal cells apparent in forebody. No eyespots or eye pigment observed. Oral sucker pyriform, slightly protruding, 119 long, 94 wide, composed of outer longitudinal muscles and inner circular muscles, inner area containing large vesicular transparent cells; mouth terminal. Acetabulum muscular, triangular in lateral view, small, 119 long, 124 wide, pre-equatorial along longitudinal axis near junction of anterior and middle thirds of body. Oral sucker to acetabulum length ratio, 1:1.0; oral sucker to acetabulum width ratio, 1:1.3. Distance between suckers, 1,099; ratio of distance between suckers to body length, 1:3.0. Prepharynx not observed. Pharynx small, 20 long, 27 wide. Esophagus 1,054 long, 9.9 wide at midpoint, straight, running almost entire length of forebody along dorsal wall of worm; esophageal wall muscular, 7 wide at posterior end. Cecal bifurcation 186 anterior to acetabulum. ‘Drüsenmagen’ (= stomach) not observed. Ceca voluminous, tortuous, consisting of series of smooth, inflated chambers filled with tan fluid, which begin anteriorly as smaller, round chambers becoming much larger, cuboidal chambers posteriorly before narrowing slightly again at posterior end. Anterior cecal chamber smallest, 123 (109–136;  $n = 2$ ) long, 29 (25–32;  $n = 2$ ) wide; middle cecal chamber largest, 182 (166–198;  $n = 2$ ) long, 246 (236–255;  $n = 2$ ) wide; posterior cecal chamber intermediate in size, 141 (131–151;  $n = 2$ ) long, 164

(149–179;  $n = 2$ ) wide. Ceca ending blindly near posterior end of body. Genital anlagen not observed. Excretory vesicle short, 50 long, 67 wide, saccular, V-shaped, surrounded by numerous gland cells; excretory arms not evident. Excretory pore terminal.

*Site of infection:* Pyloric cecum.

*Deposited specimen:* HWML voucher 49134 (1 slide).

*Remarks:* The tegument of this specimen unfortunately is contracted and damaged (2 puncture marks around mid-body). In lacking a stomach and in possessing tortuous ceca and an acetabulum, this worm appears to be a member of the didymozoid collective group type *Torticaecum*. Like *Monilicaecum*, *Torticaecum* was first given generic status by Yamaguti (1942) and is now regarded as a collective larval group name for the first free didymozoid juvenile stages that form in fish hosts (Yamaguti 1970, 1971). *Torticaecum* is distinguished from *Monilicaecum* principally by the absence of a stomach and the presence of tortuously-winding ceca in the former larval group as opposed to moniliform ceca that resemble beads on a string in the latter larval group. This specimen also can be identified as a member of *Torticaecum* in the key of Pozdnyakov and Gibson (2008) in that it possesses a pharynx and has an acetabulum that is posterior to the intestinal bifurcation, yet it lacks a stomach and gland cells around the esophagus and anterior parts of the ceca.

SUPERFAMILY HEMIUIROIDEA LOOSS, 1899

FAMILY DEROGENIDAE NICOLL, 1910

JUVENILE OF GONOCERCA PHYCIDIS (Figure 1D)

*Description:* Based on one specimen. Body cylindrical, widest at level of acetabulum, anterior extremity somewhat truncated, posterior extremity conical, 3,422 long, 791 wide at level of pharynx, 1,167 wide at level of acetabulum, 633 wide at posterior end. Esoma lacking. Forebody 1,929 long or 56% of body length, with round anterior extremity, 811 wide at level of cecal bifurcation. Hindbody wide, narrowing posterior to acetabulum, 1,493 long. Tegument smooth. Preoral lobe not observed. Oral sucker muscular, subspherical, subterminal, 596 long, 641 wide. Acetabulum muscular, round, postequatorial, large, 979 long, 900 wide. Ratio of diameter of oral sucker to acetabulum 1:1.4. Prepharynx not observed. Pharynx subspherical, 293 long, 273 wide. Esophagus not observed; cecal bifurcation immediately posterior to pharynx, 934 anterior to acetabulum. Ceca voluminous, terminating 162 or 5% of body length from posterior body end. Genital pore and other components of reproductive systems not observed. Excretory vesicle Y-shaped, with voluminous arms seen in preacetabular region running anteriorly along lateral sides of worm, ventrolateral to ceca, uniting dorsally over oral sucker. Excretory pore terminal.

*Site of infection:* Stomach.

*Deposited specimen:* HWML voucher 49135 (1 slide).

*Remarks:* This juvenile digenean was identified as the dero-genid *Gonocerca phycidis* due to the absence of an esoma, a

large acetabulum located in the posterior half of the body, ceca that end blindly, and its strikingly similar appearance to adult specimens of this species previously collected (Manter 1925, 1934). This report comprises the first record of *G. phycidis* in *G. serpens*.

NEMATODA

FAMILY ANISAKIDAE (RAILLIET AND HENRY, 1912)

ANISAKIS SP. 1 (Figure 2A)

*Description:* Based on 2 specimens. Body fusiform, robust, stout-bodied, 19.7 mm (16.2–23.2;  $n = 2$ ) long, 300 (233–366;  $n = 2$ ) wide at level of junction of esophagus and ventriculus, 451 (308–593;  $n = 2$ ) wide at midbody, 115 (112–119;  $n = 2$ ) wide at anus. Cuticle smooth, lacking lateral alae. Head width at base, 96 (82–109;  $n = 2$ ). Three lips, with dentigerous ridges, 38 (32–45;  $n = 4$ ) long, 43 (37–52;  $n = 4$ ) wide. Interlabia not observed. Prominent boring tooth (spine) 19 (12–25;  $n = 2$ ) long, 31 (20–42;  $n = 2$ ) wide at base. Esophagus muscular, 1,474 (1,347–1,600;  $n = 2$ ) long or 7% (7–8%;  $n = 2$ ) of body length, 107 (94–119;  $n = 2$ ) wide at level of midpoint. Nerve ring present, 261 (194–328;  $n = 2$ ) from anterior tip. Ventriculus oblong, 527 (472–582;  $n = 2$ ) long, 189 (149–229;  $n = 2$ ) wide. Ventricular appendage and intestinal cecum absent. Excretory pore between lateroventral lips, opening below boring tooth on ventral side. Intestine simple. Tail length (anus to posterior tip) 157 (144–169;  $n = 2$ ) long. Rectal glands oval to nearly spherical, prominent. Anus subterminal. Conical mucron (caudal spine) observed in 1 specimen, 30 long, 15 wide at base.

*Site of infection:* 1 encysted in mesenteries near junction of lower intestine and rectum; 1 unattached in pyloric cecum.

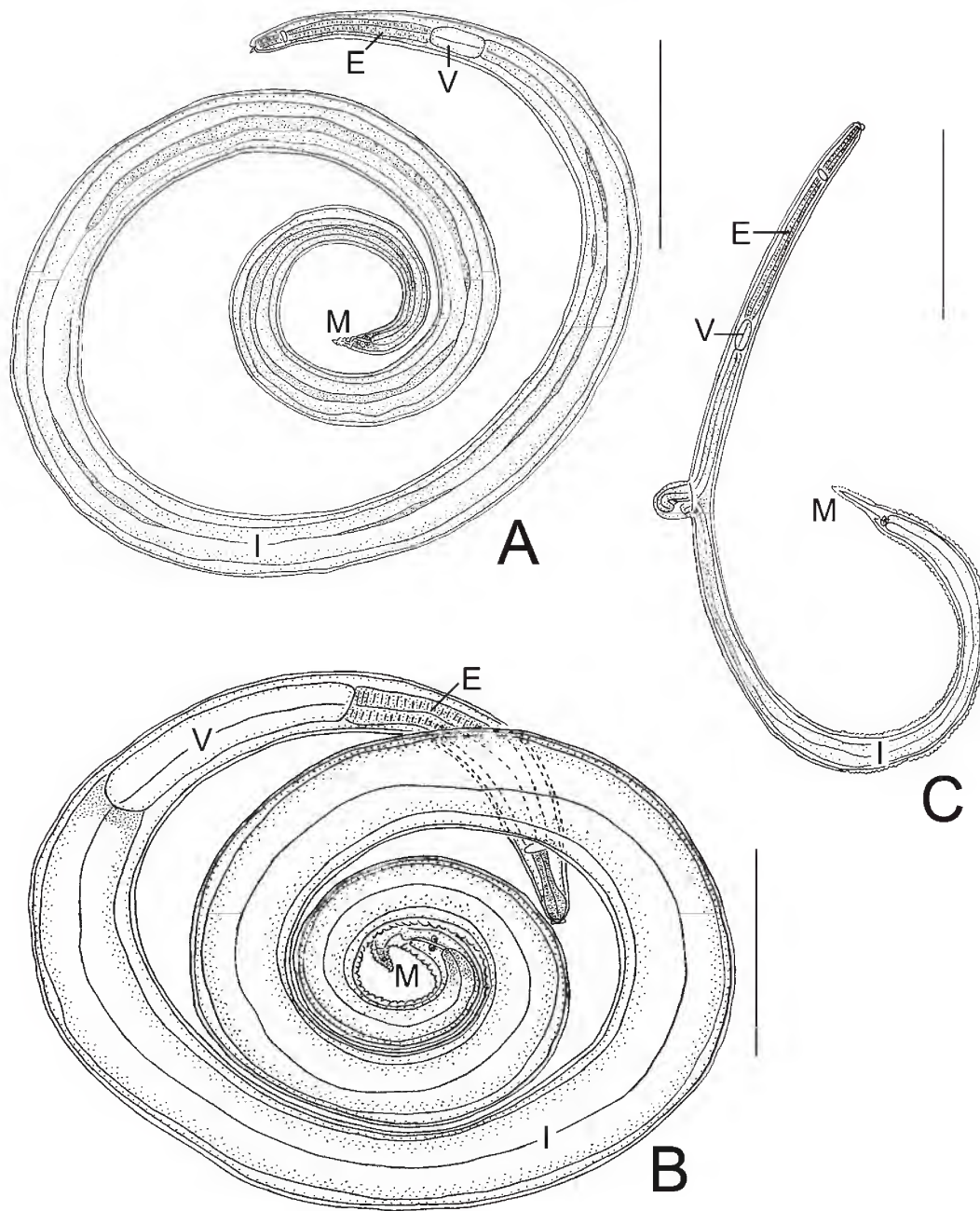
*Deposited specimens:* HWML voucher 49136 (2 slides).

*Remarks:* The presence of an oblong ventriculus lacking an appendix, no intestinal cecum, 3 lips with dentigerous ridges, no interlabia, and an excretory pore location between the lateroventral lips distinguished these nematodes as representatives of a species of *Anisakis*, and both specimens are L3 stage larvae. One appeared to have the L4 stage larva developing inside, but the lips of the latter had not erupted through the cuticle.

ANISAKIS SP. 2 (Figure 2B)

*Description:* Based on 2 specimens. Body fusiform, robust, stout-bodied, 8.524 (8,096–8,951;  $n = 2$ ) long, 170 (161–179;  $n = 2$ ) wide at level of junction of esophagus and ventriculus, 265 (243–288;  $n = 2$ ) wide at midbody, and 77 (74–79;  $n = 2$ ) wide at anus. Cuticle smooth, lacking lateral alae. Head width at base, 58 (52–65;  $n = 2$ ). Three lips, with dentigerous ridges, 24 (20–27;  $n = 5$ ) long, 27 (20–32;  $n = 5$ ) wide. Interlabia not observed. Prominent boring tooth (spine) 16 (15–17;  $n = 2$ ) long, 22 (20–25;  $n = 2$ ) wide at base. Esophagus muscular, 970 (945–995;  $n = 2$ ) long or 11% (10–12%;  $n = 2$ ) of body length, 87 (74–99;  $n = 2$ ) wide at level of midpoint. Nerve ring present, 207 (196–218;  $n = 2$ ) from anterior tip. Ventriculus cylindrical, 641 (603–680;  $n = 2$ ) long,





**Figure 2.** Illustrations of larval *Anisakis* spp. from *Gempylus serpens*.

A. *Anisakis* sp. 1, entire, lateral view. Scale bar 2 mm.

B. *Anisakis* sp. 2, entire, lateral view. Scale bar 700  $\mu$ m.

C. *Anisakis* sp. 3, entire, lateral view. Scale bar 400  $\mu$ m.

Abbreviations: E, esophagus; I, intestine; M, mucron; V, ventriculus.

165 (139–191;  $n = 2$ ) wide. Ventricular appendage and intestinal cecum absent. Excretory pore between lateroventral lips, opening below boring tooth on ventral side. Intestine simple. Tail length (anus to posterior tip) 169 (166–171;  $n = 2$ ) long. Rectal glands oval to nearly spherical, prominent. Anus subterminal. Conical mucron (caudal spine) observed in one specimen, 10 long, 7 wide at base.

*Site of infection:* Unattached in pyloric cecum.

*Deposited specimens:* HWML voucher 49136 (2 slides).

*Remarks:* The presence of a ventriculus lacking an appen-

dix, no intestinal cecum, 3 lips with dentigerous ridges, no interlabia, and an excretory pore location between the lateroventral lips characterized these nematodes as representatives of a species of *Anisakis*, and both specimens are L3 stage larvae. *Anisakis* sp. 2 differs from *Anisakis* sp. 1 in its overall smaller size and its larger ventriculus in relation to total body length; 7.5% of body length in *Anisakis* sp. 2 compared to only 2.8% of body length in *Anisakis* sp. 1.

ANISAKIS SP. 3 (Figure 2C)

*Description:* Based on one damaged specimen. Body slightly

curved anteriorly, prominently curved posteriorly, fusiform, small, 2,942 long, 77 wide at level of junction of esophagus and ventriculus, 69 wide at midbody, and 42 wide at anus. Cuticle smooth, lacking lateral alae. Head width at base, 25. Three lips, tiny, with dentigerous ridges. Interlabia not observed. Boring tooth (spine) 5 long, 17 wide at base. Esophagus muscular, 583 long or 19.8% of body length, 25 wide at level of midpoint. Nerve ring 171 from anterior tip. Ventriculus oval, small, 62 long, 37 wide. Ventricular appendage and intestinal cecum absent. Excretory pore not observed. Intestine simple. Tail length (anus to posterior tip) 114 long. Rectal glands oval to nearly spherical, prominent. Anus subterminal. Mucron (caudal spine) tiny, conical, 5 long, 3 wide at base.

*Site of infection:* Unattached in pyloric cecum.

*Deposited specimen:* HWML voucher 49136 (1 slide).

*Remarks:* The presence of a ventriculus lacking an appendix, no intestinal cecum, 3 lips with dentigerous ridges, and no interlabia characterized this specimen as a representative of a species of *Anisakis*, and the specimen is either an extremely young L3 or L2 stage larva. *Anisakis* sp. 3 differs from *Anisakis* sp. 1 and *Anisakis* sp. 2 in its longer esophagus in relation to total body length; 19.8% of body length in *Anisakis*

sp. 3 compared to 7.6% and 11.5% of body length in *Anisakis* sp. 1 and *Anisakis* sp. 2, respectively. *Anisakis* sp. 3 also differs from *Anisakis* sp. 2 in its smaller ventriculus in relation to total body length; 2.1% of body length in *Anisakis* sp. 3 compared to 7.5% of body length in *Anisakis* sp. 2.

## SUMMARY

This report documents several endohelminths not previously reported from *G. serpens*, including a cestode and a didymozoid from *G. serpens* as well as a new host record for derogenids in general and *G. phycidis* in particular. All helminths collected in this study were larvae or juveniles. We think that listing the parasites herein (Table 1) of even a single marine fish (*G. serpens*), in this case a host rarely studied for endohelminths (i.e. only 5 parasite species known from *G. serpens*), is important. This study now adds to our knowledge of marine parasites, which is quite limited compared to that of terrestrial and freshwater parasites (see Bray et al. 1999). This study also provides information regarding the diet of *G. serpens*. Stomach examination revealed 6 early juvenile flatfish (Pleuronectiformes), suggestive of pelagic feeding by *G. serpens* (Moyle and Cech 1988).

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## Recruitment and Colonization of Macroalgae to a Newly Constructed Rocky Intertidal Habitat in the Northwest Gulf of Mexico

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# RECRUITMENT AND COLONIZATION OF MACROALGAE TO A NEWLY CONSTRUCTED ROCKY INTERTIDAL HABITAT IN THE NORTHWEST GULF OF MEXICO

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**ABSTRACT:** Marine macroalgal assemblages on artificial structures play an important ecological role in coastal and estuarine ecosystems and may supplement natural communities in nearby waters. The rocky jetties of Packery Channel, located near Corpus Christi, Texas represent a recent addition of hard structure for colonization in the northwest Gulf of Mexico. The purpose of this research was to monitor the initial immigration of macroalgal species during the first year of colonization and determine the effects of wave energy on recruitment. Ten sampling sites were established along the offshore portion of the new Packery Channel jetties. Samples were taken bimonthly from along a 10 m transect between September 2006 and July 2007, with quadrats (20 x 30 cm) sampled every meter by destructive harvesting techniques. Biomass data obtained from this study assess composition and establish a timeline for algal recruitment. Within the first year macroalgal richness was found to be 40 species. Multivariate analyses show strong linkages between rate of recruitment and site location. Sites with the highest level of wave energy exhibited significantly increased biomass and simultaneous decreased richness values, indicating recruitment is affected by wave energy at a microhabitat scale.

## INTRODUCTION

Granite jetties, found along the mouth of inlets, serve to stabilize channels. By extending beyond the sandbars and breaking waves, jetties allow for calmer waters within the channels and help to stabilize the channel itself. The granite rocks also serve an additional function of providing habitat for an array of organisms. Along the Texas coast, jetties offer a significant source of hard substratum for attached macroalgae. Over 80 species of macroalgae have been reported from a single jetty community in Texas (Baca et al. 1979, Edwards 1976, Edwards and Kapraun 1973, Kaldy et al. 1995).

Dispersal of seaweed propagules, including those of macroalgae, is influenced by a variety of physical and biological factors (Gaylord et al. 2002). Coastlines exhibit complex hydrodynamic conditions such as upwelling and long-shore drift. These processes make it difficult to understand dynamics such as colonization, persistence, and post-disturbance recovery. Most seaweed propagules are able to settle immediately upon release, and the majority are thought to settle within a few days (Santelices 1990). Most long-distance transport of species is actually thought to occur via drifting plants or fertile fragments carried by currents (Chapman 1986, van den Hoek 1987).

The algal flora of Texas is largely of tropical affinity. However, there is a distinct cool temperature flora that develops during the winter and early spring (Edwards and Kapraun 1973). The result is a Texas coast with a variation of macroalgae characteristic of both the northern Gulf of Mexico (GOM) and the tropics. A recent study of the macroalgae of the Port Mansfield jetties, located about 129 km to the south of Packery Channel, reported 14 species that had not been previously recorded for the area, increasing the rich-

ness of that pass to 50 species (Klootwyk 2006). Several of these species had been previously recorded for the Port Aransas area (e.g., *Gelidium pusillum* and *Gracilaria tikvahiae*), while others had only been found to the south near Port Isabel (e.g., *Codium taylorii*). Studies are therefore needed to document the presence or absence of algal species for Packery Channel. Data from this study will aid in understanding dispersal patterns of macroalgae along the Texas coast.

The assessment of flora recruiting to jetties during the initial stages of habitat development is very important. Hard substratum provides a large vertical relief and support for dense covers of attached microalgae (periphyton), macroalgae, and epifauna (Fikes and Lehman 2008a). These communities influence food webs and affect benthic productivity by increasing the deposition of organic matter around hard structures (Atilla et al. 2003) as well as providing a food source and refuge.

Describing algal composition and colonization is an important step in understanding marine ecosystem function. There are general patterns of early colonizers, such as ephemeral algae (e.g., *Porphyra*, *Ulva*), being gradually replaced by larger perennial algae (e.g., coralline algae) (Chapman and Underwood 1998). In New South Wales, Australia, results demonstrate that there is no simple seasonal or biogeographical pattern in the development of algal assemblages, which indicate the importance of small-scale influences.

Models have been developed showing that the productivity potential of an algal-dominated system increases with decreased disturbance (Steneck and Dethier 1994). In intertidal communities this may explain cosmopolitan trends of low diversity in high energy habitats. The jetty system of Packery Channel contains varying levels of wave



energy dependant upon site location. The present study further looks at the affect of these energy levels on the colonization patterns of a developing macroalgal community.

## MATERIALS AND METHODS

### Study site

Packery Channel is located on Padre Island, near Corpus Christi, Texas and connects the GOM to the Laguna Madre (Figure 1). Construction of the jetties and the dredging of Packery Channel were completed in late September 2006. The pass and its entrance are stabilized by jetties composed of stacked granite blocks, which extend about 427 m out from the shoreline. The channel that runs the length of the pass is about 43 m wide and 3.5 m deep (U.S. Army Corps of Engineers 2003). The base of

nel completion resulted in a lack of submerged substrate suitable for algal growth. For this reason, data from sampling sites 5 and 6 are not presented. GPS waypoints were recorded for use in site identification and spray paint was applied to the granite substrate above the high tide level to mark sampled sections of jetty. This was done in order to reduce the risk of duplicate sampling at one location.

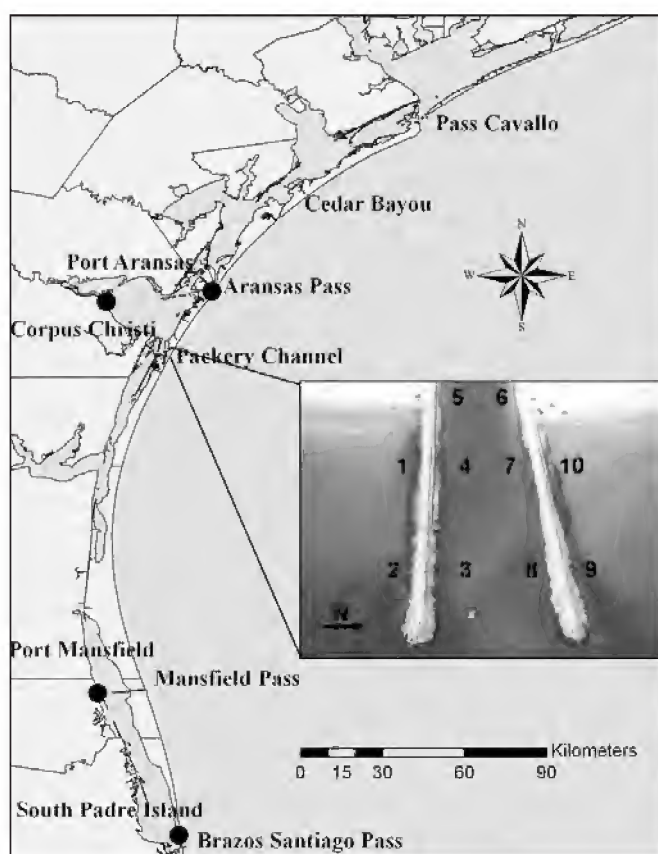
Replicates sites were identified for each of 4 energy levels: high, moderate, low, and protected. Sites 1 and 2 were considered high energy, sites 3 and 8 were considered moderate energy, sites 9 and 10 were considered low energy, and sites 4 and 7 were considered protected. A flow meter was originally used to measure differences in energy levels between sites, but was proven to be unsuccessful at those sites with large amounts of wave energy. Sites were therefore distinguished by making visual observations of wave amplitude, turbidity, and current. Due to the southeasterly nature of the winds in this region, sites to the south of the jetty system received more energy than those to the north.

Bimonthly sampling took place between 15 September 2006 and 22 July 2007. At each site, vertical transects consisting of polypropylene braided rope marked every meter were used. Transects began with the high tide line and continued over the granite substrate for 10 m (or until the granite blocks met the sandy substratum). At each marking, a 20 x 30 cm area was scraped clear of any material within the margins of a copper tubing quadrat. Spray paint was used to mark each transect location, and successive sampling events were conducted about 1 m away from the previous sampling location. The first sampling event utilized an airlift to assure that no macroalgal materials were overlooked. Material obtained from the destructive sampling was collected in pre-numbered mesh "bio-bags" (500  $\mu$ m) as it was scraped from the granite substrate. Once transferred to pre-labeled field jars, samples were preserved with 2% glutaraldehyde and seawater solution. Spatial and temporal patterns in biomass for all species were determined by analyzing dry weights.

### Data analysis

Algal biomass density ( $\text{g}/\text{m}^2$ ), expressed as the mean density from all quadrats sampled at each site for each month, was analyzed with analysis of variance (ANOVA,  $\alpha = 0.05$ ) using the general linear model procedure in SAS 9.1. We used a factorial design with 2 main fixed treatment effects, month (sampling period, 6 events), and site (position on jetty, 8 locations). The distribution of the residuals was analyzed using the UNIVARIATE procedure, and data were transformed ( $\log_{10}(x+1)$ ) to minimize heteroscedasticity. We expected to see a site-month interaction term, and therefore explored the relationship further by conducting 2 separate one-way ANOVA models if a significant interaction was observed. Mean differences among months and sites were tested using Tukey's HSD ( $\alpha = 0.05$ ).

Community data were analyzed with PRIMER v6 (Plym-



**Figure 1.** Packery Channel in relation to the Gulf of Mexico and the Texas coast. Inset: image of Packery Channel jetties with the sampling sites indicated.

the north jetty is located at 27°36.836'N, 97°12.044'W.

### Sampling techniques

Both the channel and the gulf sides of the north and south jetties were examined. Five sites were selected on each of the jetties (Figure 1); however, only 4 sites were sampled on each, 2 on the Gulf side and 2 on the channel side. This was a result of immediate sediment accumulation at 2 of the channel sites, those recessed beyond the shoreline. Accretion above the low tide mark upon chan-

**TABLE 1.** Taxonomic list of confirmed species collected for Packery Channel study. Systematics follow Wynne (2005).**Rhodophyta****CERAMIALES****Ceramiales**

*Aglaothamnion halliae* (Collins) N. Aponte, D.L. Ballant. & J.N. Norris  
*Centroceras clavulatum* (C. Agardh. in Kunth) Mont. in Durieu de

**Maisonneuve**

*Ceramium flaccidum* (Kütz.) Ardis  
*Ceramium cimbrium* H.E. Petersen in Rosenv.  
*Spyridia hypnoides* (Bory in Belanger) Papenf.

**Rhodomelaceae**

*Bryocladia cuspidata* (J. Agardh) De Toni  
*Bryocladia thyrigera* (J. Agardh) F. Schmitz in Falkenb.  
*Chondria dasyphylla* (Woodw.) C. Agardh  
*Chondrophycus poiteau* (J.V. Lamour.) K.W. Nam  
*Digenea simplex* (Wulfen) C. Agardh  
*Polysiphonia denudata* (Dillwyn) Grev. ex Harv. in Hook.

**CORALLINALES****Corallinales**

*Jania adhaerens* J.V. Lamour.  
*Haliptilon cubense* (Mont. Ex Kütz.) Garbary & H.W. Johans

**GELIDIALES****Gelidiales**

*Gelidium pusillum* (Stackh.) Le Jolis  
*Pterocladia bartlettii* (W.R. Taylor) Santel.

**GIGARTINALES****Hypneaceae**

*Hypnea musciformis* (Wulfen in Jacquin) J.V. Lamour.  
*Hypnea spinella* (C. Agardh) Kütz  
*Hypnea valentiae* (Turner) Mont.

**Solieriaceae**

*Agardhiella ramosissima* (cf.) (Harv.) Kylin  
*Agardhiella subulata* (C. Agardh) J. Agardh

**GRACILARIALES****Gracilariaceae**

*Gracilaria tikvahiae* McLachlan  
*Hydropuntia caudata* (J. Agardh) Gurgel & Frederica

**HALYMENIALES****Halymeniaceae**

*Grateloupia filicina* (J.V. Lamour.) C. Agardh  
*Grateloupia pterocladina* (M.J. Wynne) S. Kawaguchi &  
 H.W. Wang in Wang et al.

**RHODYMENIALES****Rhodymeniaceae**

*Champia* (cf.) *parvula* (C. Agardh) Harv.

**Ochrophyta****DICTYOTALES****Dictyotaceae**

*Dictyota menstrualis* (Hoyt) Schnetter, Hörnig, & Weber-Peukert

**ECTOCARPALES****Acinetosporaceae**

*Feldmania indica* (Sond.) Womersley & A. Bailey

**Ectocarpaceae**

*Ectocarpus siliculosus* (Dillwyn) Lyngb.

**Scytosiphonaceae**

*Petalonia fascia* (O.F. Müll.) Kuntze

**Chlorophyta****BRYOPSIDALES****Bryopsidaceae**

*Bryopsis pennata* J.V. Lamour  
*Bryopsis plumosa* (Huds.) C. Agardh

**CLADOPHORALES****Cladophoraceae**

*Chaetomorpha aerea* (Dillwyn) Kütz.  
*Chaetomorpha linum* (O.F. Müll.) Kütz.  
*Cladophora albida* (Nees) Kütz.  
*Cladophora dalmatica* Kütz.  
*Cladophora ruchingeri* (C. Agardh) Kütz.  
*Cladophora vagabunda* (L.) C. Hoek

**ULVALES****Ulvaceae**

*Ulva fasciata* Delile  
*Ulva flexuosa* Wulfen  
*Ulva lactuca* L.

outh Routines in Multivariate Ecological Research, Plymouth Marine Lab). Algal species were ordinated by site and date combinations, and multidimensional scaling (MDS) and hierarchical clustering with the group-average procedure were used to compare biomass values between sites and sampling months using the Bray–Curtis similarity coefficient.

A one-way analysis of similarities (ANOSIM), using individual plot biomass density ( $\text{g}/\text{m}^2$ ) data, was used to test between groups of samples by site and month. Resemblance similarity data were analyzed using Global R and p-values in a pairwise manner to compare species biomass among sites and months. SIMPER analysis was used to test for community dissimilarity between variables for sampling site and month. These data were used to break down the similarity matrix and determine which species of algae were responsible for dissimilarity between sites and months.

**RESULTS****Species richness**

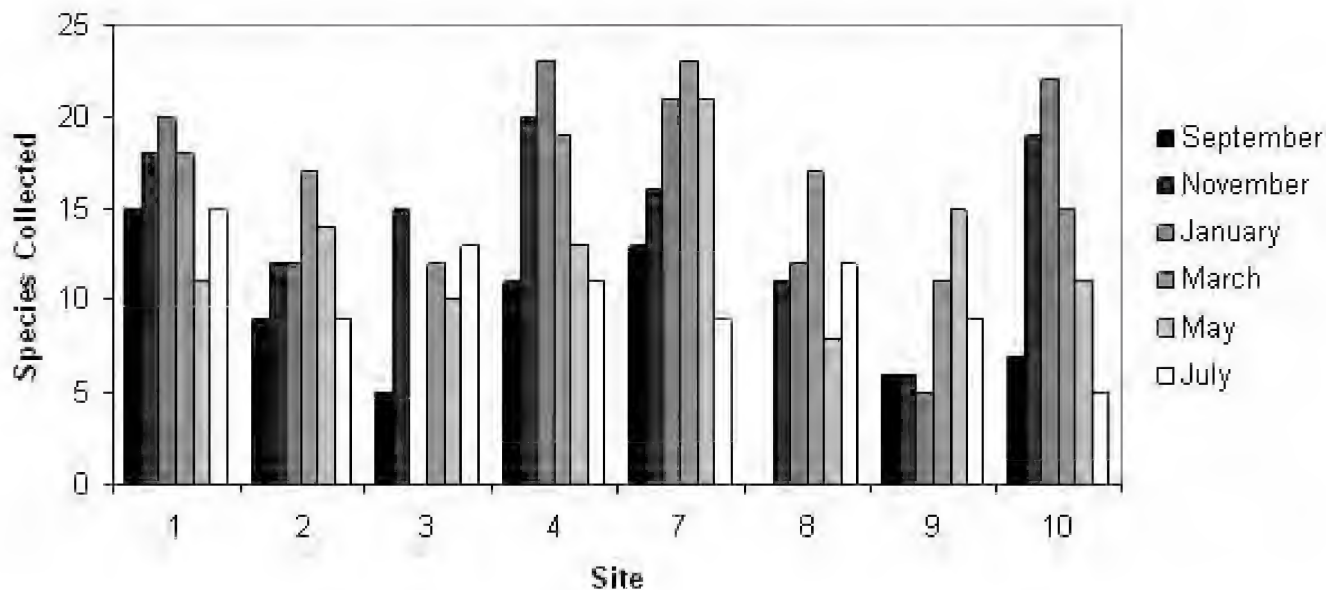
This study resulted in the initial identification and confirmation of 40 species of macroalgae growing along the rocky jetties of Packery Channel, Corpus Christi, Texas (Table 1). This represents 25 species of Rhodophyta (9 families), 4 species of Ochrophyta (4 families), and 11 species of Chlorophyta (3 families). Cheney's Floristic Ratio was found to be 9, indicating a highly tropical flora.

Species richness by sites over time showed an immediate abundance of macroalgal species occurring early in the study, indicating that a number of species were quick to recruit to the newly available granite substrate. Overall, January was the time of highest richness in this study, and species richness began to decrease after March as the warmest months of the year approached. Site 9 was the only site which did not follow these typical trends, exhibiting the highest richness in May. The sampling events with the greatest richness were site 7 in March and site 4 in January with 23 species each (Figure 2). Site 7 exhibited the overall highest richness of 33 species.

**Biomass**

A significant site–month interaction was detected in the two-way ANOVA model (ANOVA:  $F = 2.98$ ,  $df = 35$ ,  $p < 0.001$ ). This was expected, as sites colonized differently between sampling months and locations. Subsequent one-way ANOVA identified significant differences between months (ANOVA:  $F = 6.92$ ,  $df = 5$ ,  $p < 0.001$ ), with higher biomass during the cooler months (Figure 3A) and sampling sites (ANOVA:  $F = 17.14$ ,  $df = 7$ ,  $p < 0.001$ ), with higher biomass at the higher wave energy sites (Figure 3B).

The mean total algal biomass collected for this study was about  $197.4 \text{ g}/\text{month}$ . The highest overall collected grand mean algal biomass density was in March 2007 ( $112.83 \text{ g}/\text{m}^2$ ). Site 1, the highest energy site, had the highest overall collected grand mean algal biomass density of  $114 \text{ g}/\text{m}^2$ , and site 9, a low energy site, had the lowest overall collected grand mean



**Figure 2.** Species richness totals by site for each sampling month for the study.

algal biomass density of 15.5 g/m<sup>2</sup> (Figure 3). Rhodophyta made up the highest percentage of initial biomass (93.1%), followed by Chlorophyta (6.7%) and Ochrophyta (0.2%).

Monthly biomass values indicate that there was much variation in algal abundance throughout the year and between sites. Individual sites were dominated by Rhodophyta, with the exception of site 9 in March and May, where Chlorophyta was dominant. On 3 separate occurrences, all quadrats along a transect were fully devoid of algal growth, which account for a biomass of zero for that sampling event.

#### Community analysis

Cluster analysis (Bray-Curtis) for sites showed about a 48% similarity between all sites for species data, including data for the duration of the study (Figure 4). All sites, with the exception of site 9, were found to be about 57% similar. Sites 10 and 4 had the highest overall similarity (~80%), followed by sites 3 and 8 (~74%) and sites 1 and 2 (~73%).

Cluster analysis (Bray-Curtis) for sampling months revealed about a 67% similarity between all months for species data, including data for the duration of the study (Figure 5). All sampling months, with the exception of September, were found to be about 70% similar. November 2006 and January 2007 had the highest overall similarity (~83%), followed by May and July 2007 (~72%).

Pairwise comparisons revealed a highly significant site-effect on species biomass (Global  $R = 0.183$ ,  $p = 0.1\%$ ). SIMPER showed that sites 1 and 9 were the most dissimilar (98.13%) and shared only 17 similar species (Table 2). Mean within-site similarity was about 26%.

ANOSIM revealed a significant month effect on species biomass (Global  $R = 0.057$ ,  $p = 0.1\%$ ). SIMPER analysis shows that September 2006 and July 2007 were

the most dissimilar (85.92%) and shared only 16 similar species. Mean within-month similarity was about 30%.

Community analysis by site over time shows a trend in increasing community stabilization (Figure 6). Initially, sites in close proximity spatially to one another were found to exhibit up to an 80% similarity. When comparing all sites, however, they were only about 40% similar. By the end of the study, sites within close proximity were found to be no more than 60% similar, but overall similarity between sites had increased to 60% similarity. Site 9 was a clear outlier for assemblage data and was excluded in this analysis.

Second-stage MDS analysis conducted on only protected and high energy treatments showed a pronounced separation (Figure 7). Wave energy is clearly shown to affect community development.

#### Species contributions

The most abundant alga of this study was *Bryocladia thyrsgigera*, contributing the highest overall biomass with 340.6 grams dry biological weight (28.8% of overall collected biomass). *Grateloupia filicina* followed with 309.2 grams dry weight (26.1% total biomass), and *Bryocladia cuspidata* with 183.9 grams dry weight (15.5% total biomass). These three species combined made up 70.4% of the total collected biomass for this study.

Using MDS analysis and cluster overlays (percentages), many species were found to vary significantly between sites. Generally, species tended to decrease in abundance when moving from south to north, with sites 1 and 2 having the highest biomass. This was true for most top contributors, such as *B. thyrsgigera*, *B. cuspidata*, and *G. filicina*. Sites 8 and 9 exhibited some exceptions in higher biomass of some calm-water (low energy) species such as *Ulva flexuosa* and *Ectocar-*



*pus siliculosus*. Species which contributed most to overall site differentiation (SIMPER) tended to be those species that exhibited the most variation in site percent composition.

Further analysis using MDS plots and resemblance overlays showed that some species also varied significantly between sampling months. Eurythermal species such as *G. filicina* and *B. thysigera* remained present year round, whereas species such as *Petalonia fascia* and *U. flexuosa* varied considerably over the course of the year. Twenty of the 39 species examined were found to recruit during the first month after jetty completion. Only one species, *Chaetomorpha linum*, was found to recruit during the latter part of the study (July 2007).

## DISCUSSION

This study shows that bare substrate along the Texas coast colonizes rapidly and that wave energy (exposure) directly af-

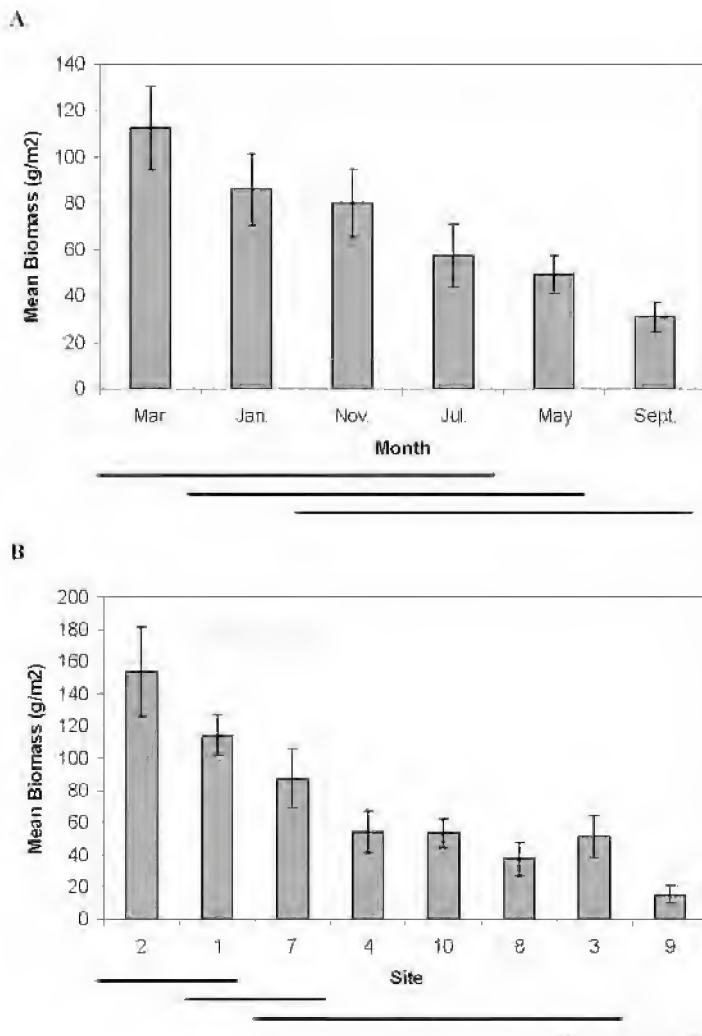
fects community structure and development in macroalgal assemblages. Species richness for this study was expected to increase over time, as would be seen in any habitat during the early stages of development. After only one year, species richness for Packery Channel (40) was found to be similar to that of Port Mansfield Pass (37) which has a well-developed macroalgal community (Klootwyk 2006). All species identified for Packery Channel have been reported from either Port Aransas, Port Mansfield, or both, with the exception of *Agardhiella ramosissima*. It is interesting to note that these data promote the idea that species recruiting to Packery Channel may come from both locales. There is also the potential for algae to recruit from additional hard substrate such as oil platforms and natural rock banks (i.e., 7 ½ Fathom Reef, about 86 km from the Packery Channel jetties).

Seasonality of macroalgae in warm-water regions is often related to temperature and desiccation (Mathieson et al. 1981, Mathieson and Penniman 1986). Species like *P. fascia* are only found during the cooler months, whereas species such as *U. fasciata* occur only during the warmer months. These shifts in species presence data directly add to the changing richness over time. Additionally, prevailing wind-driven near-shore currents along the Texas coast shift between summer and winter. These directional changes in wind-driven currents may further explain species recruitment patterns.

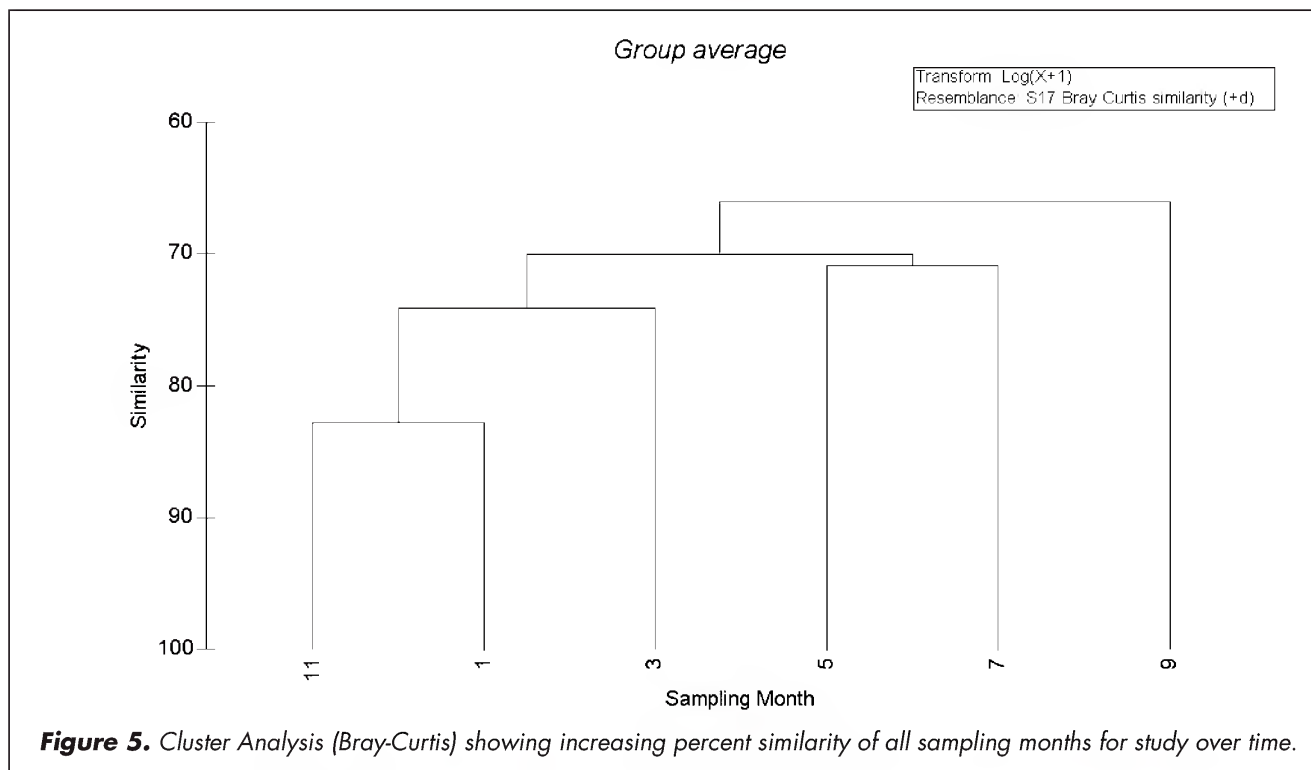
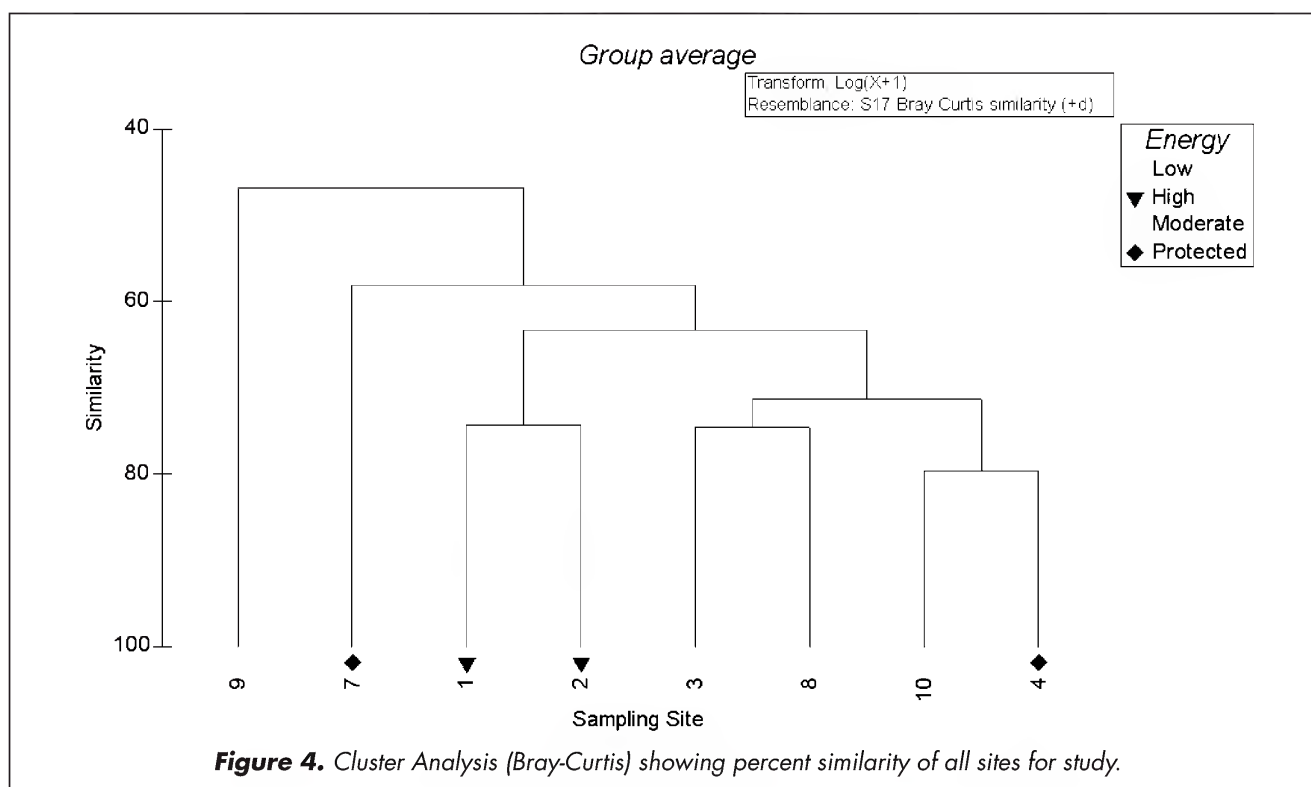
Results show an overall increase in biomass with an increase in wave energy. This indicates that energy, and not depth, determined the biomass potential for the algal community of Packery Channel. Edwards and Kapraun (1973) found that exposure to wave energy did not strongly influence species composition between sites along the Port Aransas jetties. The Port Aransas area has been described to have a richness of 88 species (Edwards 1976), much greater than Port Mansfield (37) and Packery Channel (40). Klootwyk (2006) found that sites exhibiting algal growth at greater depths also showed an overall increase in average biomass, although data taken from quadrats occupying the upper meter of the water column showed no significant difference between sites.

Cheney's Floristic Ratio was found to be 9.0 for this study which is exceptionally high when compared to other macroalgal communities from the Gulf Coast (Table 3). Temperature is the major factor controlling geographical distribution of marine algae (Edwards and Kapraun 1973) and, therefore, high ratios (meaning a more tropical flora) should be found progressing from north to south. This finding for Packery Channel may be inaccurate due to an incomplete development of the community structure since water temperature for this study ranged from 11–29.5°C (Fikes 2008), which is uncharacteristic of a tropical environment. Cheney's Floristic Ratio was designed to characterize established communities, an attribute that Packery Channel has not yet achieved.

Low biomass during late summer months is likely a result of increased stress in the form of heat and desiccation on

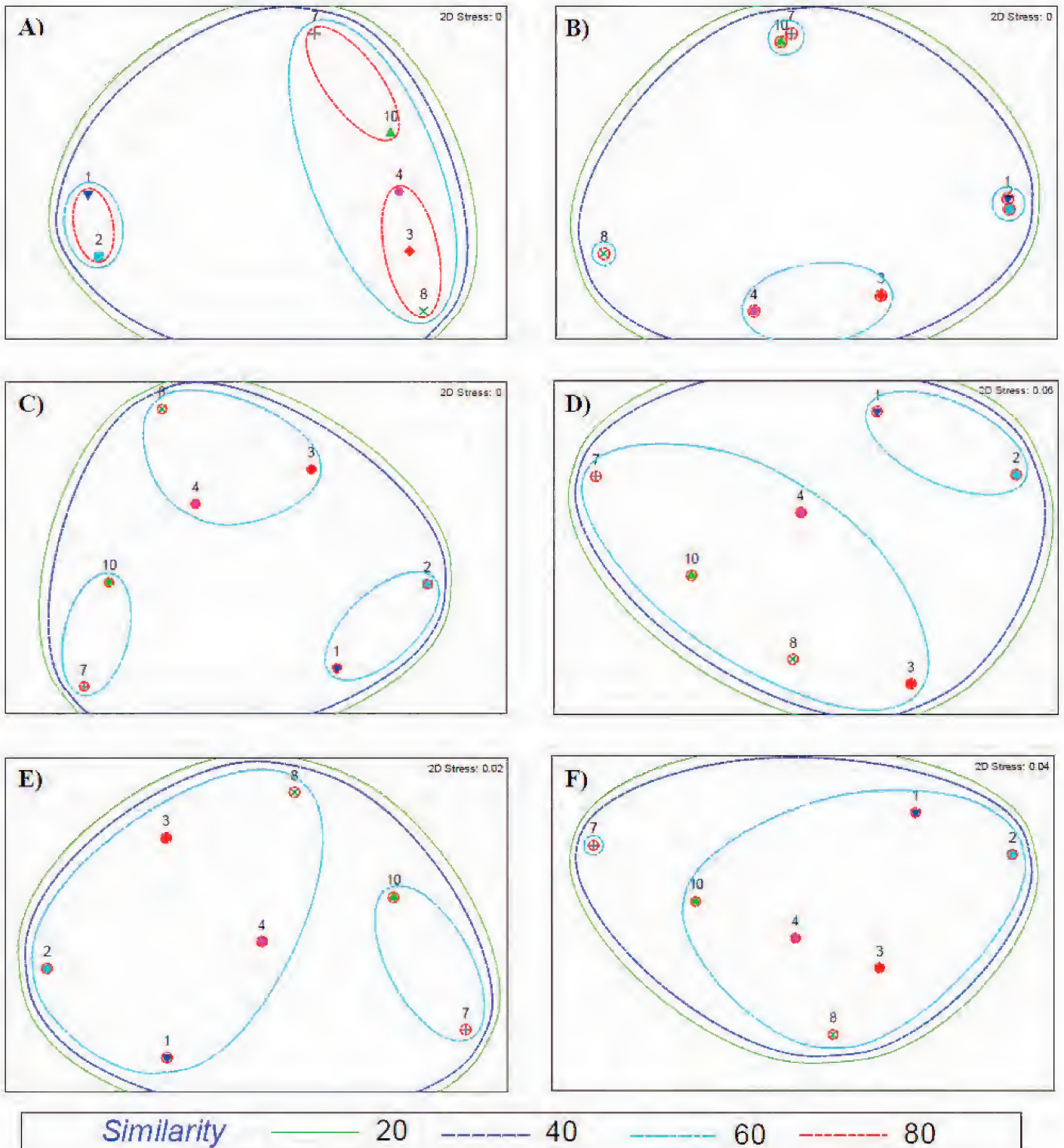


**Figure 3.** Algal biomass (grand mean  $\pm$  se) in relation to (A) sampling month for all sites and (B) sampling site for all sampling months. Sites are arranged from high energy (left) to low energy (right). Horizontal lines below graph show significant differences between months and sites (ANOVA,  $p < 0.001$ ); bars sharing lines are not significantly different (Tukey's post-hoc test  $\alpha = 0.05$ ).



macroalgal productivity (Dawes 1981, Edwards and Kapraun 1973, Round 1981, Kaldy et al. 1995). In this study biomass reached its peak during the spring, with a significant decrease in May. The overall decrease in summer biomass coincided with a decrease in species richness. Benz et al. (1979) found that there is little correlation with a single environmental factor, suggesting a synergistic effect on biomass.

Site differences in this study may be representative of varying levels of wave energy. Agan and Lehman (2001) found that Rhodophyta dominated algal coverage along the Port Aransas jetties. These authors also found that Rhodophyta abundance was greater along the channel side of the jetty (low energy) and Chlorophyta abundance was greater along the surf side (high energy). Sites with high levels of

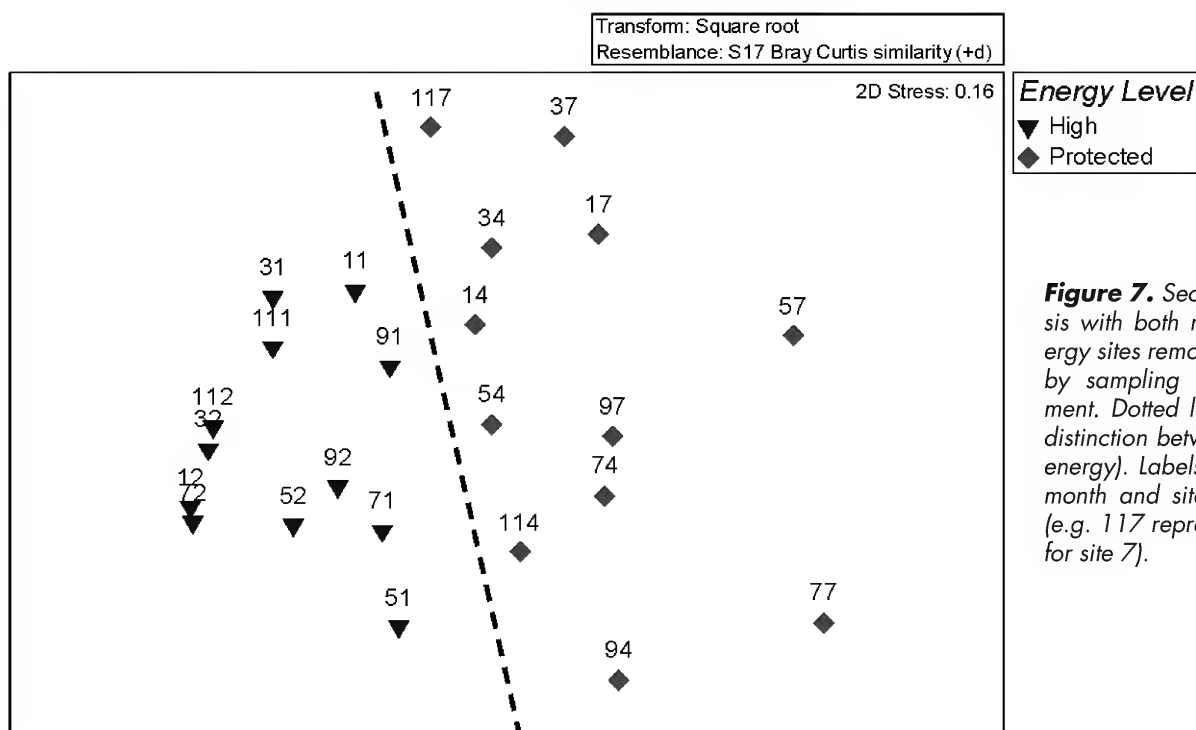


**Figure 6.** Multidimensional scaling (MDS) plots showing site similarity (two-dimensional distance) over time for the duration of the study. Each MDS plot (A-F) is based on 2 months of data and are cumulative (A = 2 mo, B = 4 mo, C = 6 mo, etc.). Numbers represent sites as in Figure 1. A. September 2006. B. November 2006. C. January 2007. D. March 2007. E. May 2007. F. July 2007.

wave energy have also been found to have increased over all biomass (Agan and Lehman 2001, Klotwyk 2006). Similar trends in biomass were observed for this study.

Quadrats sampled within a particular site showed little similarity (19.96–43.34%). Species of algae typically vary in abundance spatially and temporally, governing algal assem-





**Figure 7.** Second-stage MDS analysis with both moderate and low energy sites removed. Scaling is plotted by sampling event for each treatment. Dotted line represents a clear distinction between treatments (wave energy). Labels on plot represent the month and site for that set of data (e.g. 117 represents November data for site 7).

blages that are patchy in structure and composition (Dayton 1971, Lubchenco 1980, Jernakoff 1985, Foster 1990, Chapman and Underwood 1998). Variation in wave-exposed rocky shores has been documented when examined at a scale of replicate quadrats, sites, or shores, (Underwood and Chapman 1997) which has lead to difficulty in examining most benthic communities, including macroalgal assemblages.

Site 9 was found to be significantly different from all other sites in all aspects of this study. The stunted development of this site is likely a direct result of pass bathymetry. Data from the Texas Coastal Ocean Observation Network (TCOON) reveals that a rather large bottom depression has formed at the end of the north jetty. This pit creates an upwelling of sediments making the area more turbid than others and could account for the decreased richness and biomass. For these reasons, site 9 was excluded when looking at community dynamics of the system over time.

Increased turbidity from sediment transport in and around the channel may result in a reduction in the water depth at which algal growth occurs. Algal growth along Texas coastal jetties is known to occur at depths of up to 3 m (Britton and Morton 1989). During this study, growth was not found to occur at depths of more than about 1 m. Due to the gradual slope of the jetties at Packery Channel this "zone of algal growth" was analyzed without compromising sampling intensity.

Community analysis showed that both sampling months and sites were significantly different from one another. When compared to biomass data from Port Mansfield's macroalgal commu-

nity, it is evident that seasonal variation should not be interpreted from this study. Sampling months were all found to be about 60% similar, unlike that of Mansfield Pass, with consecutive sampling events (months) exhibiting about 80% similarity (seasonality). This inconsistency may be interpreted as macroalgal community development of Packery Channel and is not representative of true seasonal variation of an established macroalgal community.

Seven species were found restricted to either the chan-

**TABLE 2.** Average community dissimilarity (SIMPER) between all sites for Packery Channel study (given as %). Value in parentheses represents the total number of species the sites share. An \* indicates that the two sites were significantly different (ANOSIM).

Site	1	2	3	4	7	8	9	10
1	(28)							
2	59.59 (20)	(22)						
3	*81.97 (19)	*77.24 (19)	(20)					
4	*78.88 (25)	*82.74 (21)	83.33 (19)	(31)				
7	*81.71 (26)	*87.90 (20)	*90.65 (18)	*81.76 (27)	(33)			
8	*86.32 (19)	*85.15 (16)	91.26 (15)	83.34 (20)	87.12 (21)	(22)		
9	*98.13 (17)	*97.31 (17)	*96.85 (15)	*95.13 (20)	*94.43 (20)	*96.43 (17)	(20)	
10	*79.80 (23)	*83.36 (18)	*89.46 (16)	79.22 (24)	74.93 (23)	*84.94 (19)	*94.12 (19)	(26)

**TABLE 3.** Floristic affinities along the Gulf Coast (north to south) using Cheney's Floristic Ratio ( $R$ =Rhodophytes,  $C$ =Chlorophytes, and  $P$ =Phaeophytes [ $O$ =Ochrophytes]) (Cheney 1977).

Location	R	C	P (O)	Cheney	Reference
Galveston, TX	14	8	5	4.4	Lowe and Cox 1978
Port Aransas, TX	53	21	12	6.2	Edwards and Kapraun 1973
Port Aransas, TX	52	21	14	5.2	Edwards 1976
Packery Channel, TX	25	11	4	9.0	This study
Port Mansfield, TX	22	11	6	5.1	Klootwyk 2006
South Padre Island, TX	35	17	12	4.3	Sorenson 1979
South Padre Island, TX	76	36	18	6.2	Boca et al. 1979
Veracruz, Mexico	46	34	11	7.3	Lehman and Tunnell 1992

nel or surf sides of the jetties at Packery Channel. All of these species exhibited markedly low biomass values and occurred in relatively few samples. The generalization still applies that species vary in their tolerance to surf exposure (Widdowson 1964, Kapraun 1980). Energy tolerance may not be the only reason for their habitat restriction. All species with growth limited to one side or the other were also absent by the end of the study, so they may have also been limited in their range due to factors of competition.

All sites for this study (with the exception of site 9) were found to be about 55% similar in community structure. Those sites exhibiting the most similarity (e.g., sites 3 and 8, sites 1 and 2) were those with similar location along the jetties and similar levels of wave energy. These data indicate that wave energy (represented by site location and exposure) has a direct affect on colonization of algae.

Space and seawater inorganic nutrients are considered to be the limiting resources for macroalgae in most temperate systems (Chapman and Craigie 1977, Sousa 1985). Successional studies have shown that disturbance facilitates invasion of species by reducing competitors or increasing resources (D'Antonio 1993). This is especially true for intertidal habitats where disturbance affects community structure and organization (Dayton 1971). Disturbance for this study may be a result of the continued turbidity caused by resuspended sediments in and around the channel.

Although poorly studied, competition is important in most algal communities (Paine 1990) as these processes determine patterns of abundance. Important interactions occur between physical factors, grazing, and levels of inter-specific competition (Graham and Wilcox 2000). Factors and variables are constantly changing within a community, and only those species that are capable of withstanding such pressures continue to thrive. In some cases, opportunistic species rapidly colonize a habitat, and they are thus given the competitive edge for space. Several genera identified in this study have been shown to be opportunistic colonizers, such as *Hypnea* and *Ulva* (Biebl 1962, Russell and Balazs 1994).

Colonization studies should not be treated in the same manner as successional studies due to differences in factors affecting immigration to substratum. In new habitats, competition is drastically reduced and space is not initially limited. This may be the reason why early colonizers have a markedly higher biomass in proportion to other species. This study is more representative of algal colonization than secondary successional studies due to the fact that there was no established algal population in the general area of sampling. This study relies on community development from initial stages of colonization, meaning that only species with propagules in nearshore currents and adjacent habitats had the potential to recruit.

This study represented the first report of *A. ramosissima* from along the Texas coast (Fikes and Lehman 2008b). The occurrence of this species may promote the idea that though our flora shows a tropical affinity, some species may not have the means to compete with native flora. Their reproductive propagules may be present in the water column but never have the chance to stabilize within a community.

Both *B. cuspidata* and *B. thyrsgera* were found among the top three most abundant species for this study. *Bryocladia* has been found to dominate the Port Aransas, Port Mansfield, and Galveston jetties as well, indicating that it is a species of major importance along the Texas Gulf Coast (Wardle 1992). These species are typically associated with a "turf" formation, providing habitat for large numbers of benthic infauna (Valerio-Berardo and Flynn 2002). This makes them very important contributors to overall ecosystem function via bottom-up control. Bottom-up control and top-down control likely act as joint determinants of community structure in rocky intertidal communities (Menge 2000).

*Grateloupia filicina*, a species that is important commercially (Wong and Chang 2000) and ecologically, was found to be the second most abundant species collected during the study. It was also found to be the dominant species occurring at Mansfield Pass (Klootwyk 2006). This species is categorized as a thick leathery species, similar to *Gracilaria* spp., allowing

for survival in high energy environments (Littler et al. 1983). This supports the occurrence of *G. filicina* in large quantities in sites 1 and 2, those with the highest levels of wave energy.

*Hypnea musciformis* was found to be one of the top contributing species for this study, and it is known to be an early colonizer and fast-spreading species in macroalgal communities around the world. In the Hawaiian Islands, *H. musciformis* has been introduced into many communities (Russell and Balazs 1994) and has become incorporated into the diet of the green sea turtle (*Chelonia mydas* L.) which is found in great numbers throughout the Coastal Bend region, including Packery Channel.

Coralline algae are a conspicuous component of intertidal and shallow subtidal algal turfs, are among the first to recruit into these assemblages, and show a negative correlation between abundance and ephemeral coverage (Coleman 2003). *Halimnion* *cubense* and *Jania adhaerens* were both found occurring in the macroalgal turf relatively early in the study (January 2007), but their abundance was very limited. At this time many species of ephemeral algae were found occurring within the turf, possibly accounting for the low biomass of corallines. The low abundance could have also been due to the slow growth that these macroalgae typically exhibit.

The green algae *C. linum* was found to develop late in this study, and was most often found occurring in the supratidal splash zone along the jetties. Species of *Chaetomorpha*, along with *Ulva* and *Bryopsis*, are known for their ability to with-

stand partial desiccation (Biebl 1962). This element adds to the complexity and diversity of the macroalgal community of Packery Channel, as well as most rocky intertidal communities.

Few studies examine the roles of artificial habitats and their ecological role as surrogates to natural communities (Bulleri 2005). Until jetties were constructed along the Texas coast, the outer shores were limited in algal growth because they lacked the necessary hard substratum.

Previous Texas algal collections described species of *Ulva*, *Gracilaria*, *Gelidium* and *Hypnea* as the most dominant macroalgae of the Corpus Christi Bay area (Agan and Lehman 2000). These species are all found dominating the Port Aransas jetties. Representatives from each of these genera were also collected from Packery Channel, perhaps providing additional contributions to the bay community. Possible sources for these macroalgae include Corpus Christi Bay and the Upper Laguna Madre via water exchange during low tides and nearby coastal jetty communities via longshore currents.

Macroalgae immediately began to attach to the rocky substratum and these communities quickly become rich in species diversity. Though biomass values may be comparable to that of nearby systems, newly forming assemblages show pronounced patchiness in community structure. Over time these communities exhibit a more even distribution, with similar site locations showing increased similarity. An increase in energy results in both a decrease in richness and increase in biomass during habitat colonization and development.

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## Do Small, Patchy, Constructed Intertidal Oyster Reefs Reduce Salt Marsh Erosion As Well As Natural Reefs?

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# DO SMALL, PATCHY, CONSTRUCTED INTERTIDAL OYSTER REEFS REDUCE SALT MARSH EROSION AS WELL AS NATURAL REEFS?

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**ABSTRACT:** One ecological service that oyster reefs provide is stabilization of shorelines through reduced wave energy and erosion from boat traffic, storms, and predominant wind direction. Additionally, increasing sedimentation can enhance the growth of emergent marsh vegetation which further stabilizes unconsolidated sediments. A 21 mo study of constructed (with only 30-35% coverage) and natural oyster reefs in 3 bayous in the Grand Bay National Estuarine Research Reserve (NERR) suggested constructed reefs benefit this retrograding deltaic ecosystem. The marsh edge adjacent to all constructed reefs was less eroded (mean = 0.043 m) than edges adjacent to natural reefs (mean = 0.728 m), although all natural and constructed sites, regardless of bayou, illustrated large variations in marsh edge growth. The marsh edge in constructed sites in one bayou retreated more than in the other bayous, most likely due to its coarser sediments, greater boat traffic, and its apparent higher energy location within the landscape. By the end of this study, the ecological function of constructed oyster reefs in all bayous, as measured by marsh edge erosion reduction, was equivalent or exceeded the function in nearby natural oyster reefs. The physical structure of the reef further served to reduce erosion and marsh loss and this approach may be useful for management of a retrograding deltaic estuarine ecosystem like the Grand Bay NERR.

## INTRODUCTION

Eastern oyster, *Crassostrea virginica*, reefs once thrived in the coastal environments of the Atlantic and Gulf of Mexico (GOM) but have declined as a consequence of overharvesting and environmental degradation, exacerbated by disease, epizootics, and altered water flow (Breitburg et al. 2000, Coen and Luckenbach 2000, LaPeyre et al. 2003). This loss has not only resulted in diminished harvestable oysters but also plays an important role in the overall degradation of estuaries. Oyster reefs provide fundamental biological, physical, and chemical functions (Rodney and Paynter 2006, Coen et al. 2007, Nestlerode et al. 2007; Beck et al. 2009) that contribute to the persistence of estuarine ecosystems. Because of the economic and ecological value of this specialized habitat, projects have been conducted at multiple scales to restore subtidal and intertidal oyster reefs to their historical extent. Data on fringe (Cake 1983; hereafter referred to as small), intertidal reefs suggest that they provide unique and necessary habitat for resident and transient estuarine fauna as well as shoreline stabilization (Meyer et al. 1997, Bartol and Mann 1999, Meyer and Townsend 2000, Piazza et al. 2005).

The three-dimensional structure of oyster reef habitat, with its high surface area and abundant interstitial space, enhances the value of a reef by: 1) encouraging the settle-

ment of oyster spat and other sessile organisms that promote the growth and physical expansion of the habitat (Tolley and Voley 2005, Rodney and Paynter 2006, Powell and Klinck 2007, Gregalis et al. 2008, Gregalis et al. 2009); 2) attracting a diversity of infaunal and epifaunal organisms (Powers et al. 2003, Tolley and Voley 2005, Shervette and Gelwick 2008a); 3) increasing prey biomass available to predators, thereby enhancing trophic transfer (Meyer and Townsend 2000, Tolley and Voley 2005, Rodney and Paynter 2006); 4) providing a shallow water refuge in times of stress, such as desiccation stress and seasonal hypoxia (Lenihan et al. 2001) or parasite infestation (LaPeyre et al. 2003); and 5) creating physical barriers that enhance sediment deposition and buffer wave energy, thus increasing marsh area and reducing shoreline erosion (Meyer et al. 1997, Piazza et al. 2005, Coen et al. 2007). These functions become compromised with the large-scale loss of oyster reefs (Hargis and Haven 1999, Boesch et al. 2001, Beck et al. 2009).

Although oyster reefs are an ecologically and economically valuable estuarine habitat type, few studies have focused on restoration of and ecological services provided by small, intertidal reefs that thrive in the shallow estuaries along the GOM (Piazza et al. 2005, Tolley et al. 2005, Shervette and Gelwick 2008a, b). As part of a larger restoration project

(Peterson and Stricklin 2008), we examined one ecological service of oyster reefs, marsh edge vegetation stabilization and growth, within three bayous of the Grand Bay National Estuarine Research Reserve (NERR), located in southeast Jackson County, Mississippi. We tested the hypothesis that small, intertidal constructed oyster reefs have similar or enhanced shoreline protection capability as nearby natural reefs.

## MATERIALS AND METHODS

### Site description

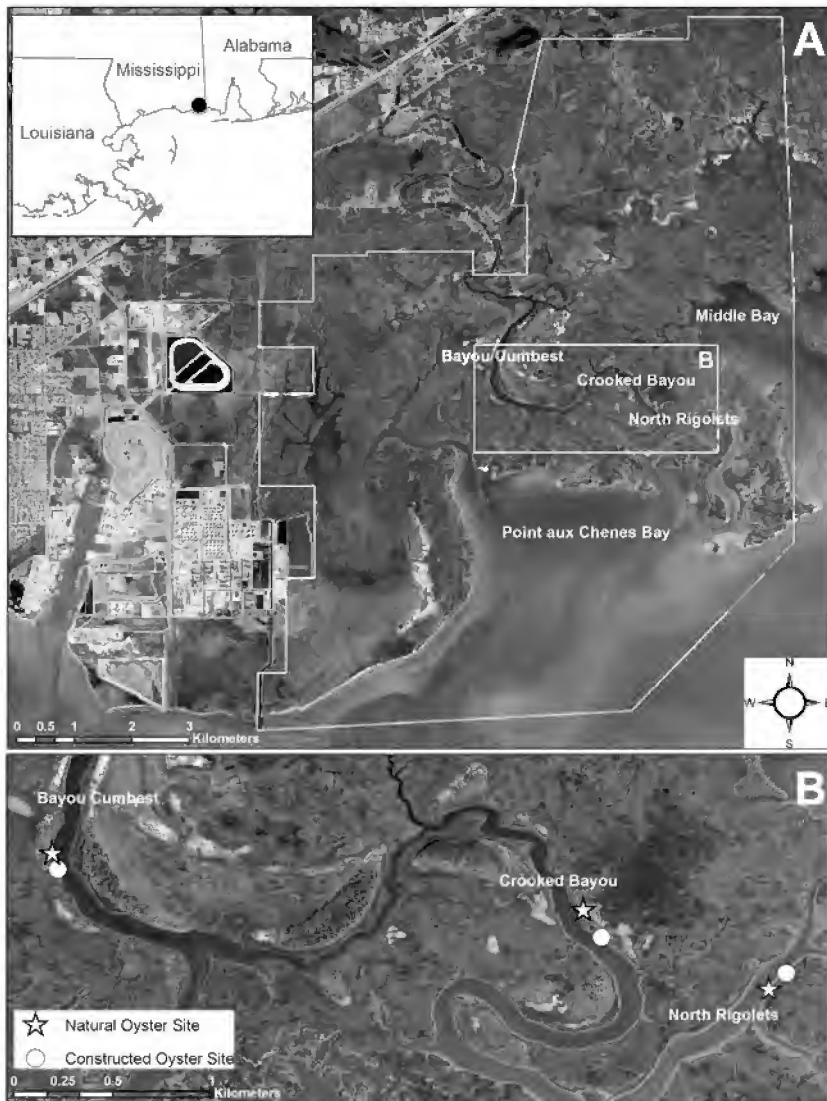
Replicate sites in intertidal areas were selected to construct oyster reefs and examine shoreline change based on

est, Crooked Bayou, and North Rigolets (Figure 1). Grand Bay NERR is a marine dominated ecosystem (Peterson et al. 2007) with freshwater input occurring via precipitation, runoff, and inflow from Bayou Cumbest. Tides are microtidal ( $\sim 0.5$  m) and can be wind-driven. The Grand Bay NERR is a retrograding delta with marsh erosion rates ranging from 0.5–4.0 m/yr, with much of the system experiencing rates of  $> 2.5$  m/yr (Otvos 2007). Bayou Cumbest is the farthest inland of the three bayous with a well-consolidated clay and sand shore adjacent to a steep, upland erosional marsh edge consisting of *Spartina alterniflora* and *Juncus roemerianus*. Crooked Bayou is the middle bayou with a poorly consolidated muddy bottom, and is adjacent to *S. alterniflora*. North Rigolets is located between Point aux Chenes Bay and Middle Bay, is composed of unconsolidated mud, and is adjacent to *S. alterniflora*.

### Reef construction and sampling procedures

Within each bayou, we constructed 55.8 m<sup>2</sup> (30.5 m x 1.8 m) intertidal oyster reefs on 17–18 August 2006, and each was set at least 92 m away from a paired nearby natural reef. Each paired set was subject to similar physical conditions within each bayou, and each reef location (constructed or natural) was divided into 3 contiguous sections which served as replicates. Within each of these sections, an equal-sized grid of cells was visualized to facilitate the placement of trays (48.26 cm L x 30.48 cm W x 11.43 cm H; Norseman Plastics) with shell bags and/or shell bags alone (max mesh size = 25.4 mm; same dimensions as trays) during initial reef construction. To simulate the observed patchiness in natural reefs, the constructed reefs were supplemented with shell bags or trays with shell bags (see Peterson and Stricklin 2008 for details on biological assessment component) filled with about 0.03 m<sup>3</sup> (1 ft<sup>3</sup>) of oyster cultch to reach the desired 30–35% coverage (a total of 34 bags and trays per section). Shell bags were laid flat on top of the mudflat and trays were dug into the mudflat to be no higher than shell bags, but both were about 15 cm (6 in) above the mudflat. The trays with shell bags and shell bags were deployed in the intertidal zone between high and low tide, and bags were cut open to mimic natural habitat.

The ability of oyster reefs to enhance marsh edge stabilization and growth was assessed using marsh edge stabilization profiles (Meyer et al. 1997). A mid-line transect on each natural and constructed reef replicate section ( $n = 3$ ) was established with a PVC stake in the marsh



**Figure 1.** Sampling sites. A. Map of the Grand Bay National Estuarine Research Reserve, Jackson County, MS and the three bayous sampled. B. Close-up of the locations of the constructed and natural oyster reef pairs in the three bayous.

adjacent available oyster habitat, water flow, salinity, substrate, and slope suitable for natural seeding and development of self-sustaining reefs (Cake 1983) in three bayous of the Grand Bay NERR (30°23'N, 88°24'W): Bayou Cumb-



**TABLE 1.** Summary of water quality conditions pooled over the course of the study ( $\bar{x} \pm 1$  se). There were no significant differences among bayou or habitat for any variable over the course of the study.

Bayou	Habitat	Temp (°C)	Salinity	DO (mg/L)
Bayou Cumbest	Constructed	20.23 $\pm$ 2.67	20.87 $\pm$ 2.16	7.02 $\pm$ 1.21
	Natural	20.45 $\pm$ 2.64	21.33 $\pm$ 2.12	5.70 $\pm$ 0.61
Crooked Bayou	Constructed	21.04 $\pm$ 2.31	24.16 $\pm$ 1.63	6.46 $\pm$ 0.96
	Natural	21.27 $\pm$ 2.41	24.29 $\pm$ 1.47	6.57 $\pm$ 0.74
North Rigolets	Constructed	19.87 $\pm$ 2.46	25.06 $\pm$ 1.59	5.81 $\pm$ 0.95
	Natural	20.02 $\pm$ 2.45	25.10 $\pm$ 1.67	5.93 $\pm$ 0.96

and a PVC stake within the water but immediately upland of the reef boundary. Marsh edge growth was measured as the change in distance (m) between the upland pole and the edge of the marsh grass along the midline transect for each pole set. We attempted to be accurate with measurements of the poles on each sampling event but there may have been some minor error in these measurements over time and space. These data were analyzed as the change in distance over time in comparison to the initial distance measured in August 2006. Monitoring was conducted quarterly over a 21 mo period from November 2006 through June 2008. Salinity, water temperature (°C), and dissolved oxygen (mg/L) were measured once per sampling event at each reef location with a YSI model 85 handheld meter.

#### Data analysis

Water temperature, salinity and dissolved oxygen were averaged over date and compared with a 2-way ANOVA with bayou and habitat as main effects. Results were considered significant if  $p \leq 0.05$  and all data were tested for normality and homogeneity of variance prior to ANOVA. All 3 variables met these assumptions.

Marsh edge growth was examined between habitat type (natural,  $n = 3$  and constructed,  $n = 3$  reefs) and bayou ( $n = 3$ ) (between-subjects factors) and across time (quarters,  $n = 7$ ) (within-subjects factor) with a split-plot ANOVA (Green and Salkind 2008). If a significant F-value was noted for the between-subjects component of the analy-

sis, mean values were evaluated with a post-hoc Sidak test. For the within-subject component, we adjusted the degrees of freedom with the Greenhouse-Geisser epsilon value (Field 2005, Green and Salkind 2008). Significant F-values for within-subject factors (change over time) were followed up with paired-t tests between all possible time periods, and adjusted

with a sequential Bonferroni technique (Rice 1989), reducing the chance of a Type I error in making multiple pairwise comparisons. However, because Bonferroni adjustments are very conservative, we chose to balance making a Type I or Type II error by using  $p = 0.10$ ; data were analyzed using SPSS (version 15.0). Results were considered significant if  $p \leq 0.05$  except where noted above and all data were tested for normality and homogeneity of variance prior to ANOVA. Data for marsh edge growth were untransformed. Also, if a significant interaction term was indicated for the between-subjects main effects, the F-values and partial eta squared (partial  $\eta^2$ , effect size) values were compared to aid in interpreting the importance of the main effects relative to the interaction term(s). Partial  $\eta^2$  is the proportion of the total variation attributable to a factor excluding the other main and interaction factors (Green and Salkind 2008). The values range from 0 to 1, with higher numbers having a greater effect size. For consistency, all interaction terms are presented in the B x H (i.e., bayou x habitat type) format. One of the marsh edge transect poles was vandalized from one constructed site in Bayou Cumbest in May 2007 limiting the analysis to only 2 replicates from that point forward.

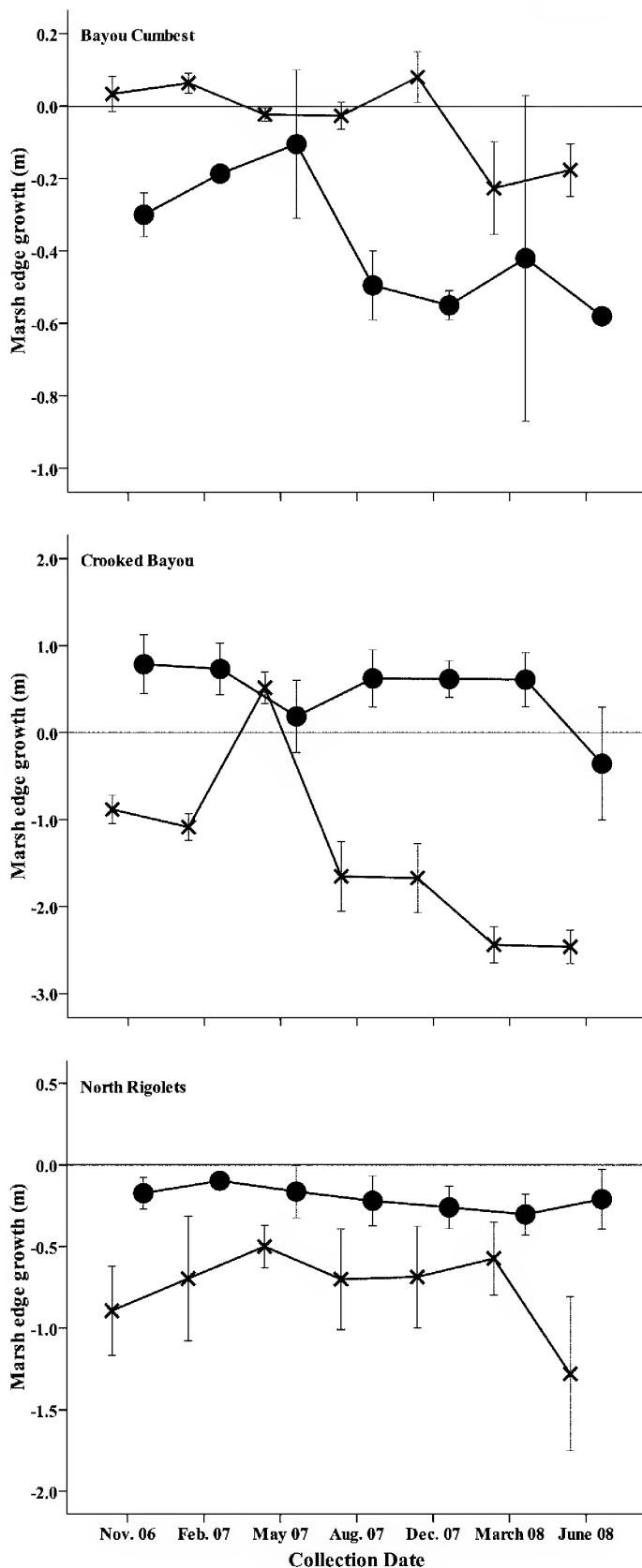
#### RESULTS

Water temperature, dissolved oxygen and salinity between bayou and habitat (constructed and natural) were similar and not significantly different ( $p > 0.05$ ) over the course of this

**TABLE 2.** Summary of split plot ANOVA statistics, the follow-up Sidak pairwise multiple comparisons (between-subjects), and paired-t tests (within-subjects). B = bayou, H = habitat, Q = reverse time (quarter), BC = Bayou Cumbest, CB = Crooked Bayou, NR = North Rigolets, C (c) = constructed, N (n) = natural. Quarter (time): 1 = November 2006, 2 = February 2007, 3 = May 2007, 4 = August 2007, 5 = December 2007, 6 = March 2008, 7 = June 2008. Bold values are significantly different within columns.

Measure	Overall test p-value (F-value, partial $\eta^2$ )	Bayou comparison (% distance $\pm 1$ se)	Habitat (% distance $\pm 1$ se)	Quarter (time)
Marsh edge distance (m)	B = 0.389 (1.031, 0.158) <b>H = 0.002 (17.066, 0.608)</b> <b>B*H = 0.001 (14.353, 0.723)</b> <b>Q &lt; 0.001 (12.988, 0.541)</b> <b>B(Q) &lt; 0.001 (4.926, 0.472)</b> <b>H(Q) &lt; 0.001 (5.274, 0.324)</b> <b>B*H(Q) &lt; 0.001 (6.782, 0.552)</b>	BC > CB > NR (BC: -0.212, 0.154) (CB: -0.463, 0.138) (NR: -0.483, 0.138)	<b>C &gt; N</b> (C: -0.043, 0.122) (N: -0.728, 0.113)	BCc BCn <b>CBc = 1&gt;4</b> <b>CBn = 1&gt;(6=7), 3&gt;2</b> NRc NRn





**Figure 2.** Plots of change in marsh edge growth (m,  $\pm 1$  se) since August 2006 by bayou ( $n = 3$ ) and habitat type ( $n = 2$ ) over the course of the study. Plotted measurements by habitat are offset laterally from the dates for clarity; actual sampling was conducted over a 1-2 day period during all events. Note the different y-axis scales for the three graphs. For some dates, se was smaller than the size of the symbol used for the mean value. ● - constructed sites; X - natural sites.

study (Table 1). The lowest temperatures were observed in November 2006 and December 2007 (11.9–14.5°C) and the highest in August 2007 and June 2008 (26.5–29.8°C). Dissolved oxygen varied 3.37–13.60 mg/L in Bayou Cumbest, 2.87–9.70 mg/L in Crooked Bayou and 2.37–10.40 mg/L in North Rigolets. Salinity varied 18.4–29.1 in Crooked Bayou and 18.3–28.8 in North Rigolets, and Bayou Cumbest had the lowest salinity (11.6–29.3).

There was an overall erosion of marsh edge over the course of this study at all sites. Although no differences were noted among bayous (Table 2), marsh edge growth did vary significantly between constructed and natural oyster reefs within all three bayous and over time in Crooked Bayou (Figure 2). This variation was accounted for by significant interaction effects among combinations of bayou, habitat and time (quarter), but each had small  $F$ -values and moderate partial  $\eta^2$  values (Table 2). For example, in Bayou Cumbest marsh edge advanced at the constructed reef through May 2007 and retreated during the remainder of the study. In natural reefs, the marsh edge did not change through December 2007 and then retreated through June 2008 (Figure 2). In contrast, Crooked Bayou marsh edge growth was stable in constructed reefs over time except June 2008 (Figure 2), but natural reefs had positive marsh edge growth between February and May 2007, though overall reductions occurred between November 2006 and June 2008 (Figure 2, Table 2). In North Rigolets, there was slow retreat of marsh edge in the constructed reefs over time while the natural reefs exhibited high variability and an overall retreat over time (Figure 2). Overall, there were significant main effects of habitat, time, and  $B \times H$  interaction effects, with high  $F$ -values and moderate to high partial  $\eta^2$  values (Table 2), indicating less retreat of the marsh edge in the constructed reefs compared to the natural reefs in all bayous (Table 2). The greatest source of variation was associated with the interaction effect of bayou  $\times$  habitat (Table 2), with Bayou Cumbest exhibiting more retreat of the marsh edge in constructed versus natural reefs. In contrast, Crooked Bayou and North Rigolets marsh edge retreat was more pronounced in natural relative to constructed reefs (Figure 2). Variability (larger se) in marsh edge growth in natural reef sites was greater than constructed sites in North Rigolets and Crooked Bayou compared to Bayou Cumbest (Figure 2). Mean overall marsh edge retreat was 0.728 m for natural and 0.043 m for constructed oyster reefs.

## DISCUSSION

One goal of habitat restoration is to develop a functional habitat where one did not previously exist, or to rehabilitate a degraded habitat (Simenstad et al. 2006) such that system productivity and ecosystem services are enhanced. We determined that constructed oyster reefs slowed the rate of erosion more than nearby natural reefs in the Grand Bay NERR; mean marsh edge retreat was 0.035 m/mo (0.728

m overall) for natural and 0.002 m/mo (0.043 m overall) for constructed oyster reefs. This pattern varied by bayou, however, with the least overall marsh edge retreat at Bayou Cumbest, followed by Crooked Bayou and North Rigolets. Though there were temporal differences noted on all reefs among the three bayous, these changes were most visible at the natural reefs in Crooked Bayou and constructed reefs in Bayou Cumbest. Rates of retreat were similar to that found by Piazza et al. (2005) in Louisiana, who reported a mean overall retreat of 0.08 m/mo (1.68 m overall) in added cultch sites and 0.12 m/mo (2.52 m overall) in non-cultched sites. Though there was no overall mean growth in the marsh edge (except Bayou Cumbest natural sites), the reduced retreat in marsh edge adjacent to constructed oyster reefs highlights the ability of these reefs (representing only 30–35% coverage) to reduce shoreline erosion under the environmental conditions at our sites. It is possible that greater oyster shell coverage on these small intertidal reefs may further retard erosion or enhance sediment accretion and thus growth of the marsh edge.

We had three concerns about our marsh edge growth measurements. First, the PVC posts used for marking the upland to lowland transect may have been subject to movement due to weather and wave action because some stakes during the course of the study appeared to be leaning a bit out of the vertical. To minimize inter-observer variability, we had the same individuals make each set of measurements. Second, short-term studies such as this one may not encompass the full spectrum of conditions, which may have revealed sustained advances or retreats in marsh edge at constructed reefs over a longer time period. A North Carolina study of similar duration (Meyer et al. 1997; 20 mo) found little difference between cultched and non-cultched reefs. However, Meyer et al. (1997) reported a mean advance of 0.26 m over 20 mo, with growth varying by reef location

(orientation to wind and wave action); a greater percent cover of oyster shell was also used compared to the Grand Bay NERR sites. Clearly, longer study duration would allow for more accumulation or erosion of sediments along the marsh edge; however, the construction of reefs with oyster cultch within Grand Bay NERR appears to provide some protection of salt marsh shorelines, as has been found in Louisiana (Piazza et al. 2005). Finally, differences existed in sediment composition between sites that may have influenced sediment accretion patterns and erosion. Bayou Cumbest sites had more consolidated clay/sandy sediments whereas at the other two locations, sediments were unconsolidated and muddy. North Rigolets and Crooked Bayou exhibited more erosion than elsewhere, most likely from orientation to the constant southeast wind direction and the fact that Bayou Cumbest had a bit more protection from upland trees than the other two locations. This is consistent with findings by Piazza et al. (2005), who proposed that intertidal reefs work better to stabilize marsh edge in low energy than high energy sites.

As ecosystem engineers (Jones et al. 1994, Micheli and Peterson 1999), oysters and the reefs they create provide habitat and stabilize shorelines by buffering wave energy and mitigating erosion caused by boat traffic, storms, and predominant wind direction. Furthermore, by increasing rates of sedimentation they can enhance the growth of emergent marsh vegetation thereby further stabilizing unconsolidated sediments (Coen et al. 1999, Mann 2000, Piazza et al. 2005). By the end of the study, the ecological function of the constructed reefs, as measured by reduction in marsh edge erosion, was equivalent or exceeded the function of nearby natural oyster reefs. The use of small, intertidal reefs to reduce marsh retreat may be a useful management tool to mitigate retrograding deltaic estuarine ecosystems like the Grand Bay NERR.

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Observations on the Kalliapseudid Tanaidacea (Crustacea: Malacostraca: Peracarida) from the Northwestern Atlantic, with an Illustrated Key to the Species

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# OBSERVATIONS ON THE KALLIAPSEUDID TANAIIDACEA (CRUSTACEA: MALACOSTRACA: PERACARIDA) FROM THE NORTHWESTERN ATLANTIC, WITH AN ILLUSTRATED KEY TO THE SPECIES

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**ABSTRACT:** New information for the kalliapseudid Tanaidacea occurring in the northwestern Atlantic is presented and discussed, including data on range extensions and new depth ranges for 4 species. The taxa studied came from the shelf and coastal waters of the southeastern United States, Puerto Rico and Trinidad. The occurrence of *Mesokalliapseudes bahamensis* Sieg is extended from the Bahamas and Belize to the coastal waters of East and Gulf coasts (South Carolina to West Florida). The range of *Psammokalliapseudes granulosus* Brum is expanded northward into the eastern Gulf of Mexico and new locality records for this species are established for Tobago and Puerto Rico. *Mesokalliapseudes brasiliensis* (Băcescu), previously known from the southwestern Atlantic off Brazil, is reported from the coastal waters off Trinidad. The range of *Tanapseudes gutui* Hansknecht, Heard, and Bamber is expanded northward into the eastern Gulf of Mexico. New depth ranges are established for *Alokalliapseudes macsweenyi* (Drumm) (82 m), *M. bahamensis* (52 m), *P. granulosus* (53 m), and *T. gutui* (82 m). An offshore form of *A. macsweenyi* occurs at depths ranging from 10-82 m on the inner and mid continental shelf off the west coast of Florida (Gulf of Mexico); it differs from the coastal form by the shape and dentition of the male and female chelipeds. Synonymies, diagnoses, life history remarks, and an illustrated key to the seven kalliapseudid species known from the NW Atlantic are presented.

## INTRODUCTION

Currently 41 species representing 12 genera and 3 subfamilies comprise members of the tanaidacean family Kalliapseudidae Lang, 1956 (Anderson 2009, Drumm et al. 2009). Kalliapseudids are distributed throughout the world's tropical, subtropical, and temperate coastal waters and with few known exceptions, are restricted to depths of less than 200 m (D.T. Drumm, pers. obser.). Within estuarine and shelf waters of the north Atlantic region the family is presently comprised of 6 nominal species contained in 4 genera and 2 subfamilies.

In an unpublished master's thesis, McSweeney (1968) presented the first well-documented discovery for a kalliapseudid from the NW Atlantic. His detailed and well-illustrated description for "*Kalliapseudes* sp. A" [now *Alokalliapseudes macsweenyi* (Drumm, 2003)] was based on specimens from southeastern Florida. The report of Gardiner (1973) for *Cirratodactylus floridensis* Gardiner, 1973 (now *Psammokalliapseudes granulosus* Brum, 1973) represents the first published record for the family from the region. Since then, descriptions and records for 4 additional kalliapseudids, *Mesokalliapseudes bahamensis* Sieg, 1982, *M. soniadaunae* Bamber, 1993, *M. thalasispeleus* Guțu, 2006; and *Tanapseudes gutui* Hansknecht, Heard and Bamber, 2002 from the northwestern Atlantic region have been published.

This report deals with a review and the presentation of new information on the occurrence of members of the family Kalliapseudidae from the northwestern Atlantic. Besides new range and locality records, we present diagnoses, synon-

ymies, an illustrated key, and remarks on the life histories, ecology and taxonomy for the kalliapseudid species known to occur in the northwest Atlantic region. The information presented here will be invaluable to future studies on the ecology, biogeography and phylogeography of the Kalliapseudidae. This paper was borne partly out of the senior author's dissertation on the systematic revision of the tanaidacean family Kalliapseudidae.

## MATERIALS AND METHODS

The total length (TL) of specimens was measured from the tip of the rostrum to the tip of the pleotelson. Material from the Mississippi-Alabama-Florida Outer Continental Shelf Study (MAFLA) has been retained at the Gulf Coast Research Laboratory (GCRL) Museum, Ocean Springs, MS, USA. Morphological terminology follows Larsen (2003). Synonymies of described species, including references to pages and figures in original descriptions, are listed immediately underneath each species.

Abbreviations for museums, institutions and research programs used: GCRL, Gulf Coast Research Laboratory; MAFLA, Mississippi-Alabama-Florida Outer Continental Shelf Study; MHN, Museum National d'Histoire Naturelle, Grigore Antipa, Romania; MZUSP, Museu de Zoologia, Universidade de São Paulo; NHM, Natural History Museum, London, UK; NMW, National Museum of Wales, Cardiff, UK; SCDNR, South Carolina Department of Natural Resources; SERTC, Southeastern Regional Taxonomic



Laboratory, Charleston South Carolina; USNM: National Museum of Natural History, Smithsonian Institution, Washington DC, USA; ZMK: Zoologisches Museum der Christian-Albrechts-Universität, Kiel, Germany.

## RESULTS AND DISCUSSION

### Systematics

SUBORDER APSEUDOMORPHA SIEG, 1980

FAMILY KALLIAPSEUDIDAE LANG, 1956

SUBFAMILY KALLIAPSEUDINAE LANG, 1956

GENUS ALOKALLIAPSEUDES GUȚU, 2006

*Mesokalliapseudes* Lang, 1956 (in part)

**Revised Diagnosis:** Antenna third article with ventromedial smooth and blunt triangular projection; last peduncle article lacking double row of plumose setae. Mandibular palp terminally with setulate seta shorter than others. Cheliped sexually dimorphic (male propodus more robust and with differing cutting edge dentition compared to female); exopodite absent. Pereopod 1 lacking exopodite. Pereopods 2 and 3 dactylus with thin, proximal digitiform prolongation ending in sensory setae; unguis absent. Pereopods 4 and 5 dactylus short and terminating in tuft of sensory setae; unguis absent. Pereopod 6 dactylus sexually dimorphic (longer in males) and with one subterminal seta. Pleopod exopodite biarticulate. Pleotelson with two terminal long plumose setae. Uropod exopodite with one small round basal article and two larger distal articles.

**Remarks:** GuȚu (2006) elevated all four of Lang's (1956) *Kalliapseudes* subgenera to full generic rank and erected the monotypic genus *Alokalliapseudes* to receive *Kalliapseudes* (*Mesokalliapseudes*) *macsweenyi* Drumm, 2003. GuȚu (2006) distinguished *Alokalliapseudes* from *Mesokalliapseudes* primarily by the presence of sexually dimorphic chelipeds. The generic status of *Alokalliapseudes* is presently being reevaluated by one of us (DTD) using both morphological and molecular criteria.

*ALOKALLIAPSEUDES MACSWEENYI* (DRUMM, 2003) (Figures 1–3, 14B, D, E)

*Kalliapseudes* (*Mesokalliapseudes*) *macsweenyi* Drumm 2003: 1–12, figures 1–5

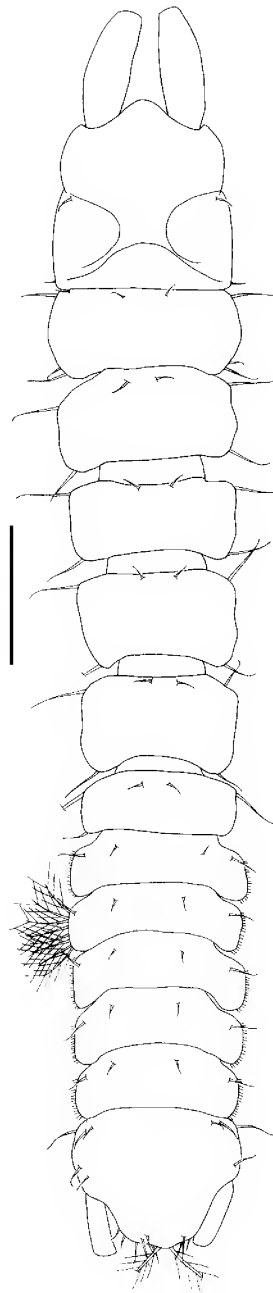
*Kalliapseudes macsweenyi*: Drumm 2004: 137; 2005:203.

*Alokalliapseudes macsweenyi* GuȚu 2006: 159, figures 253–261

*Kalliapseudes* sp. A McSweeney 1968: 28–40, figures 1–7.

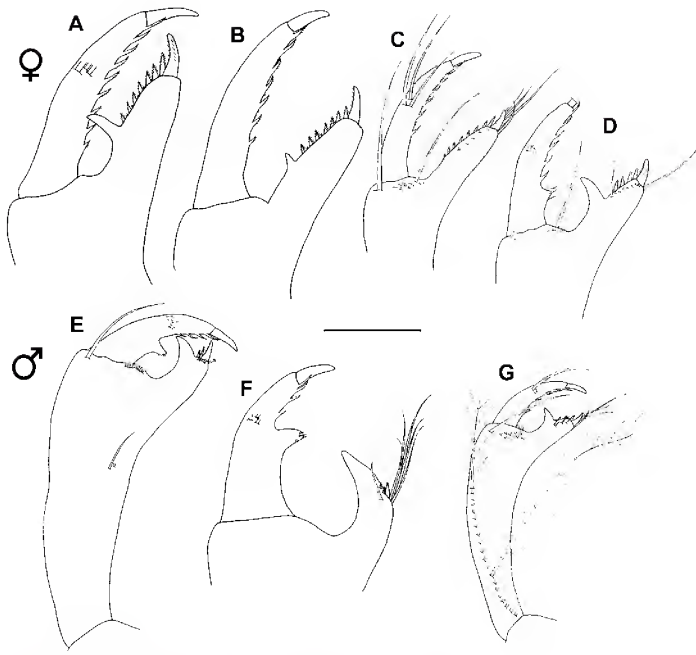
**Diagnosis:** Fully diagnosed and described by Drumm (2003).

**Material Examined:** Coastal and near shore sites; Paratypes (USNM 1016974, 5 females and 5 males), NW Atlantic, John U. Lloyd State Park, Whiskey Creek, Dania Beach, FL, tidal creek draining mangrove habitat running parallel to beach, 26°05'N, 80°06'W, 0.5 m depth; 3 males and 2 females (USNM 107021), Alligator Harbor, Franklin



**Figure 1.** *Alokalliapseudes macsweenyi* 'offshore morph,' dorsal view of adult male (lateral pleonite setae mostly shown only by their bases). Scale bar = 0.5 mm.

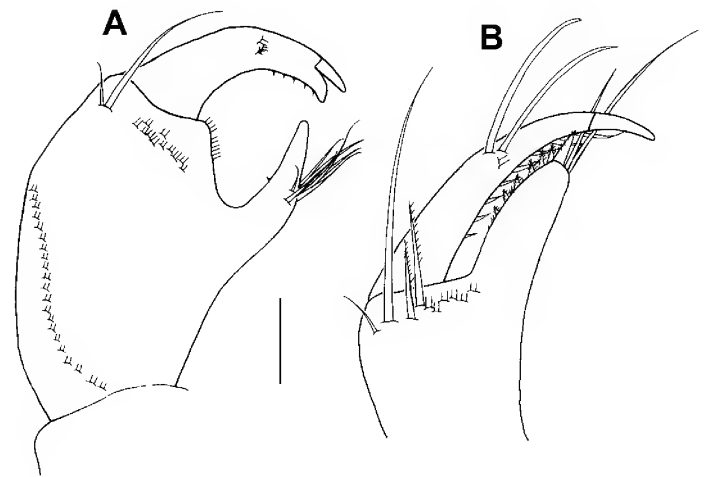
County, FL, littoral sand-mud bar, 6 June, 1960, coll. & ident. C.E. King; several adult males and females were examined in the following locations: Ft. Pierce, FL, 27°30'N, 80°20'W; Long Key, FL, 24°49'N, 80°48'W; Tampa Bay, FL, 27°37.9'N, 82°39.4'W; Panama City, FL, 30°09'N, 85°41'W; Horn Island, MS, 30°15'N, 88°43'W; Petit Bois Island, MS, 30°12'N, 88°25'W. Off shore sites (all from the MAFLA); Adult female with oostegites, Station 2747, 27°24.2'N, 84°07.3'W, 74 m, medium fine sand, September 1977; adult male, station 2211, 27°56'29.5"N, 83°52'59.5"W, 43 m, coarse sand, February 1978; 2 adult females and 1 adult male (4.2 mm TL), station 2640, 29°43'29.3"N, 87°54'30.3"W, 35 m, medium sand, September 1977; 2 adult females and 2 adult males, station 2104–05, 26°25'N, 83°23'00.8"W, 53 m, coarse sand, November 1977; 1 male, 1 female, 2 juveniles, station 2104–06, 26°25'N, 83°23'00.8"W, 53 m, coarse sand, November 1977; 2 males, station 2104–07, 26°25'N, 83°23'00.8"W, 53 m, coarse sand, November 1977; 1 female, 4 males, 3 juveniles, station 2104–08, 26°25'N, 83°23'00.8"W, 53 m, coarse sand, November 1977; 6 females, 1 juvenile, station 2104–10, 26°25'N, 83°23'00.8"W, 53 m, coarse sand, November 1977; 2 females with oostegites, station 2104–11, 26°25'N, 83°23'00.8"W, 53 m, coarse sand, November 1977; 1 male, station 2104–G, 26°25'N, 83°23'00.8"W, 53 m, coarse sand, September 1975; 1 female with oostegites, 1 juvenile, station 2207–3, 27°57'00.4"N, 83°09'00.3"W, 19 m, fine-very fine sand, November 1977; 2 females, station 2207–05, 27°57'00.4"N, 83°09'00.3"W,



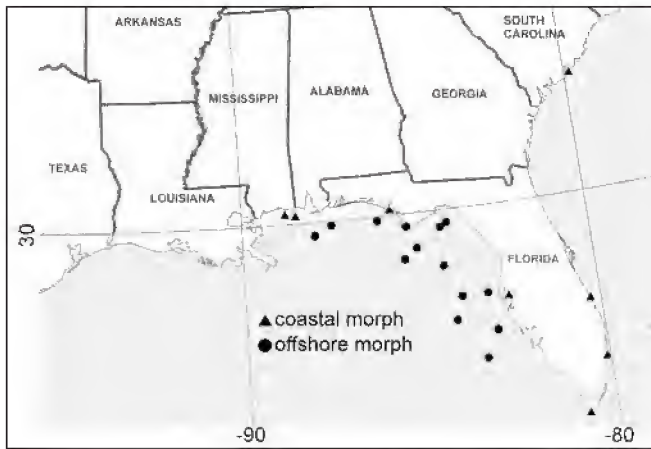
**Figure 2.** Chelipeds of *Alokallipseudes macsweenyi* 'offshore morph'. A-C. Female with oostegites. D. Ovigerous female. E, F. Adult male. G. Subadult male. Scale bar = 0.2 mm.

19 m, fine-very fine sand, November 1977; 4 juveniles, station 2207-07, 27°57'00.4"N, 83°09'00.3"W, 19 m, fine-very fine sand, November 1977; 2 males, station 2207-10, 27°57'00.4"N, 83°09'00.3"W, 19 m, fine-very fine sand, November 1977; 1 juvenile, station 2207-11, 27°57'00.4"N, 83°09'00.3"W, 19 m, fine-very fine sand, November 1977; 1 ovigerous female, station 2211-08, 27°56'29.5"N, 83°52'59.5"W, 43 m, coarse sand, February 1978; 1 female with oostegites, station 2316-J, 28°42'00.3"N, 84°20'00.7"W, 35 m, silty fine sand, November 1977; 1 female with oostegites, 1 female with emptied marsupium, 1 male, 3 juveniles, station 2419-C, 29°46'59.8"N, 84°05'00.2"W, 10 m, medium fine sand; 1 female with oostegites, station 2419-D, 29°46'59.8"N, 84°05'00.2"W, 10 m, medium fine sand, February 1975; 2 females, 1 male, 1 juvenile, station 2419-E, 29°46'59.8"N, 84°05'00.2"W, 10 m, medium fine sand, February 1975; 1 female with oostegites, 3 males, 1 juvenile, station 2419-F, 29°46'59.8"N, 84°05'00.2"W, 10 m, medium fine sand, February 1975; 1 ovigerous female, station 2419-Z, 29°46'59.8"N, 84°05'00.2"W, 10 m, medium fine sand, February 1975; 1 ovigerous female, station 2423-A, 29°37'00.8"N, 84°17'00.2"W, 19 m, silty fine sand, 1975; 1 male, station 2423-F, 29°37'00.8"N, 84°17'00.2"W, 19 m, silty fine sand, September 1977; 1 female with oostegites, 1 male, station 2423-G, 29°37'00.8"N, 84°17'00.2"W, 19 m, silty fine sand, February 1975; 1 male, station 2423-H, 29°37'00.8"N, 84°17'00.2"W, 19 m, silty fine sand, 1976; 1 male, 1 juvenile, station 2423-I, 29°37'00.8"N, 84°17'00.2"W, 19 m, silty fine sand, February, 1975; 1 juvenile, station 2423-K, 29°37'00.8"N, 84°17'00.2"W, 19

m, silty fine sand; 1 female with oostegites, station 2424-B, 29°13'00.7"N, 85°00'01.4"W, 27 m, medium sand, 1976; 1 female, station 2424-I, 29°13'00.7"N, 85°00'01.4"W, 27 m, medium sand, February 1975; 1 male, station 2426-E, 28°57'59.4"N, 85°23'00.2"W, 82 m, fine sand, 1975; 2 females with oostegites, station 2528-C, 29°54'58.6"N, 86°04'58.5"W, 37 m, coarse sand; 1 female with oostegites, 1 male, station 2528-J, 29°54'58.6"N, 86°04'58.5"W, 37 m, coarse sand, February 1978; 1 male, station 2533-C, 29°42'59.9"N, 85°15'28.6"W, 67 m, coarse sand; 1 female with oostegites, station 2642-E, 29°40.5'N, 87°37'W, 36 m, medium sand; 2 females, 2 juveniles, station 2747-10, 27°24.2'N, 84°07.3'W, 74 m, medium fine sand, August 1977; 4 males, 2 juveniles, 1 manca, 27°24.2'N, 84°07.3'W, 74 m, medium fine sand, August 1977; 2 females, station 2748-03, 27°37.2'N, 83°53.5'W, 50 m, coarse sand, November 1977; 1 female with oostegites, 1 male, station 2748-05, 27°37.2'N, 83°53.5'W, 50 m, coarse sand, August 1977; 1 female, 1 male, 1 juvenile, station 2748-06, 27°37.2'N, 83°53.5'W, 50 m, coarse sand, August 1977; 1 female with oostegites, 1 male, station 2748-06, 27°37.2'N, 83°53.5'W, 50 m, coarse sand, February, 1978; 2 juveniles, station 2748-06, 27°37.2'N, 83°53.5'W, 50 m, coarse sand, November 1978; 1 female, station 2748-07, 27°37.2'N, 83°53.5'W, 50 m, coarse sand, August 1977; 1 male, station 2748-07, 27°37.2'N, 83°53.5'W, 50 m, coarse sand, November 1977; 1 female, station 2748-09, 27°37.2'N, 83°53.5'W, 50 m, coarse sand, November 1977; 1 female with oostegites, 2 males, station 2748-11, 27°37.2'N, 83°53.5'W, 50 m, coarse sand, November 1977; 1 ovigerous female, station 2851, 27°03'25.8"N, 83°01'08.5"W, 36 m, fine sand; 1 male, station 2856-E, 29°54'01.3"N, 87°24'00.2"W, 30 m, fine sand; 1 subadult male, station 2856-F, 29°54'01.3"N, 87°24'00.2"W, 30 m, fine sand, September 1977; 1 male, sta-



**Figure 3.** Chelipeds of *Alokallipseudes macsweenyi* 'coastal morph' from Ft. Morgan, Alabama. A. Adult male. B. Female with oostegites. Scale bar = 0.2 mm.



**Figure 4.** Map showing the distribution of *Alokalliapseudes macsweenyi*. Black circles represent the 'offshore morph' and triangles indicate the 'coastal morph.'

tion 2856-H, 29°54'01.3"N, 87°24'00.2"W, 30 m, fine sand, September, 1977; 1 male, 1 juvenile, station 2856-J, 29°54'01.3"N, 87°24'00.2"W, 30 m, fine sand, September 1977.

**Geographic distribution:** NW Atlantic (South Carolina to Florida Keys), eastern Gulf of Mexico (GOM) (northward to coastal Mississippi), bathymetric range: 0.5–82 m (Figure 4).

**Remarks:** The 'offshore morph' of *A. macsweenyi* can be distinguished from the 'coastal morph' most notably by differences in the male cheliped. The propodus of the male cheliped for the 'coastal morph' (Figure 3A) is much more robust and is short (less than 2 times as long as broad, excluding fixed finger), while the propodus of the 'offshore morph' is long (more than 2 times as long as broad) (Figure 2E). The dactylus cutting edge of the 'coastal morph' does not have a medial tooth as in adult males of the 'offshore morph.' The terminal claw of the fixed finger of the propodus in the 'offshore morph' can either be of regular size (Figure 2E) or reduced (Figure 2F). Subadult males have a propodus shape similar to females (Figure 2G).

The females of both forms are nearly identical; however, the fixed finger cutting edge of the 'coastal morph' (Figure 3B) has rarely been observed to possess a proximal tooth. This tooth can be large (Figure 2A), or small (Figure 2B) in the 'offshore morph.' However, several of the females examined, especially ovigerous females, lacked this tooth (Figure 2C). One 'offshore morph' female with oostegites had a small setose tooth on the dactylus cutting edge (Figure 2D).

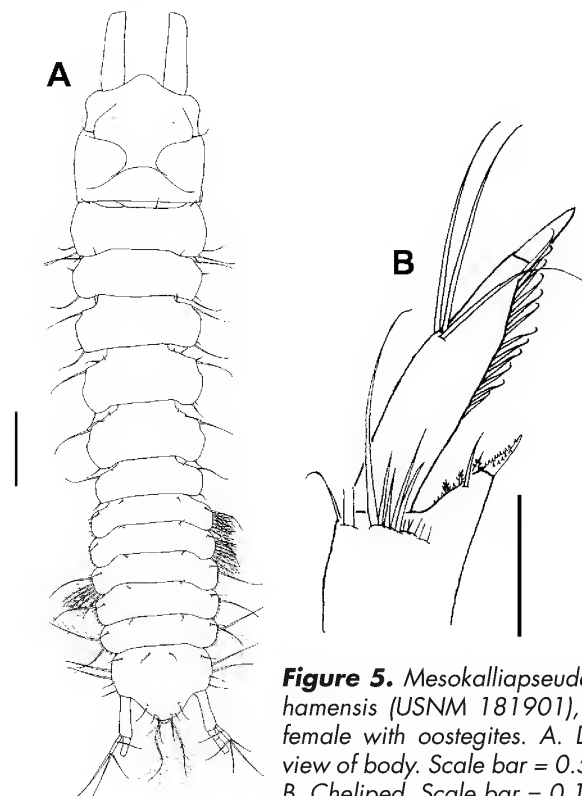
Examination of material from the eastern GOM revealed the presence of a new 'morph' of *Alokalliapseudes macsweenyi*, which generally occurred in offshore sites and greater depths than the inshore 'coastal morph'. The morphs can generally be distinguished by differences in the cheliped. McSweeney (1968) in an unpublished MS thesis noticed that a small percentage of females of *A. macsweenyi* collected in

the Biscayne Bay area of South Florida had a small tooth proximally on the fixed finger cutting edge. However, the senior author has examined numerous specimens of the 'coastal morph' throughout its range and has never seen this tooth on the fixed finger. Since both forms of the female cheliped are apparently represented in offshore and coastal habitats, we are hesitant to call the 'offshore morph' a separate species (although one form is much more common in one region than the other, and vice versa). It is often difficult to quantify variation within a species, hence the reason many biologists are skeptical about the subspecies category. Whether one agrees with subspecies or full species status, it is clear that the 'offshore morph' is distinct enough to suggest specific separation from the 'coastal morph.' It would be interesting to determine whether these phenotypic differences are associated with genetic isolation. This species might be diverging and undergoing incipient speciation. The present pattern suggests that selection is favoring one form over the other in different habitats. The pattern of the adult male cheliped of the 'offshore morph' could be attributed to paedomorphosis (the retention of juvenile characteristics in the adult) because the juvenile males of the 'coastal morph' have a slender cheliped propodus as seen in the adult males of the 'offshore morph.' This warrants further investigation.

GENUS *MESOKALLIAPSEUDES* LANG, 1956

*Kalliapseudes* (*Mesokalliapseudes*) Lang 1956: 216.

*Mesokalliapseudes*: Guțu 2006: 142.



**Figure 5.** *Mesokalliapseudes bahamensis* (USNM 181901), adult female with oostegites. A. Dorsal view of body. Scale bar = 0.5 mm. B. Cheliped. Scale bar = 0.1 mm.



**Diagnosis** (modified after Guțu 2006): Accessory flagellum of antennule with 3 or 4 articles. Antenna peduncle without double row of plumose setae on last article. Cheliped without exopodite; propodus slender and very long, much longer than carpus, fixed finger shorter than dactylus. Pereopod 1 without exopodite. Pereopods 2 and 3 dactylus with long and thin outer proximal digitiform prolongation, with few sensory setae. Pereopods 4 and 5 short and thick with some sensory setae; unguis absent. Pereopod 6 dactylus with subterminal seta. Pleopod exopodite biarticulate. Pleotelson with two terminal long plumose setae. Male with cheliped similar to female.

**Remarks:** The distribution of this genus occurs exclusively in the New World. Four of the 6 species occur in the northwest Atlantic and the other 2 occur in the northeast Pacific (on the west coast of Baja California, Mexico). *Mesokalliapseudes* is characterized from the other genera within the subfamily Kalliapseudinae by the following combination of characters: 1) last peduncle article of antenna lacking double-row of plumose setae, 2) male and female cheliped with very long and slender propodus and with an apparent lack of sexual dimorphism, and 3) absence of exopodites on the cheliped and first pereopod.

*MESOKALLIAPSEUDES BAHAMENSIS* SIEG, 1982 (Figures 5, 14A, C, G, I)

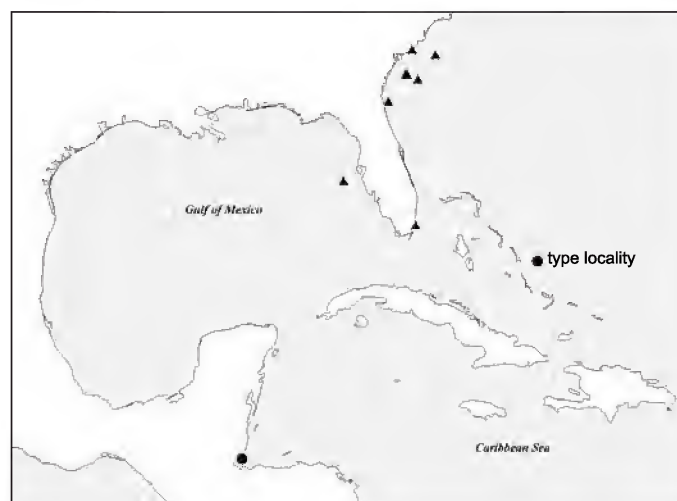
*Kalliapseudes* (*Mesokalliapseudes*) *bahamensis* Sieg 1982: 3–10, figures 1–4; Bamber 1993: 122; Drumm 2003: 2, 11.

*Kalliapseudes bahamensis* Bamber 1993: 128–130, figure 5.

*Mesokalliapseudes bahamensis* Guțu 2006: 142, 148, 150, 151, figures 232–235.

**Type material:** Holotype female (USNM 181707), paratypes (93 juveniles and 69 females, USNM 181901), paratypes (17 juveniles and 14 females, ZMK Tan. 40).

**Material examined:** Paratypes (USNM 181901), San Salvador, Bahamas, inside NW reef, near Dump Reef, 24°08'N, 74°28'W 4 m, 18 December 1979; Kiawah Island, SC, 32°29'6"N, 78°49'18"W, S121, SERTC Invert. Collection, SCDNR, 52.0 m, coll. David Knott, 6 August 1981, 1 ovigerous female (dissected) ~ 6.5 mm, 3 females with emptied marsupium, 3 females with oostegites, 3 subadult females and 1 subadult male; offshore disposal area, Charleston, SC, 32°42'30"N, 79°51'36"W, S98, SERTC Invert. Collection, SCDNR, 8–17 m, coll. David Knott, August 1978, 1 subadult female; off Savannah River, GA, 31°44'6"N, 80°13'0.1"W, S116, SERTC Invert. Collection, SCDNR, 33 m, coll. David Knott, 21 August 1980, 1 female with emptied marsupium and 1 subadult male; off Little Tybee Island, GA, 31°41'6"N, 80°20'48"W, S119, SERTC Invert. Collection, SCDNR, 28 m, coll. David Knott, 10 March 1981, 1 subadult male; off Amelia Island, FL, 30°37'00.12"N, 81°10'41.8"W, S117, SERTC Invert. Collection, SCDNR, 22 m, coll. David Knott, 4 August 1980, 4 subadult males ~ 3.7 mm. 1 adult female; GOM, 27°37'2"N, 83°53'5"W,



**Figure 6.** Map showing the distribution of *Kalliapseudes bahamensis*. Black circles represent previously published records and triangles indicate new distribution locations.

MAFLA, 50 m, 9 August 1977.

**Diagnosis:** (Adult) Rostrum rounded. Pereonites without anterolateral apophyses. Pleotelson broader than long. Third peduncle article of antenna spinulate. Mandibular palp terminally with simple seta. Fixed finger of propodus of cheliped less than one half length of dactylus; cutting edge of dactylus with more than 10 long setae increasing in length distally.

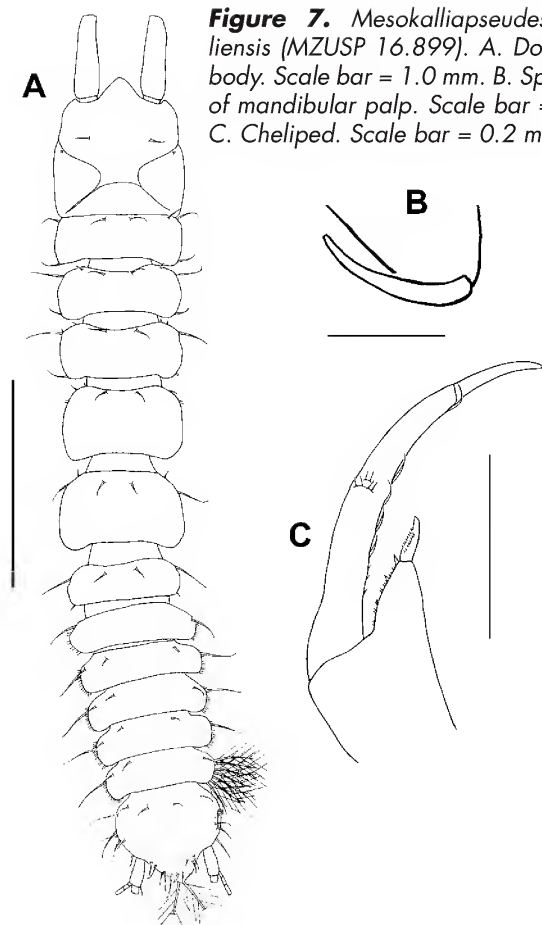
**Type locality:** San Salvador, Bahamas, inside NW reef, near Dump Reef, 24°08'N, 74°28'W (Figure 6).

**Geographic distribution:** NW Atlantic and Gulf of Mexico, from South Carolina to southeast Florida (new locality records), San Salvador Bahamas, Caribbean Sea (Carrie Bow Cay, Belize), bathymetric range: 4–52 m (Figure 6).

**Remarks:** Examination of material from the collections of SERTC confirmed the presence of *M. bahamensis* in the coastal and shelf waters off South Carolina, Georgia, and northeastern Florida. Additional specimens of this species were also made available by Judy Johnson, Nova Southeast University, from shallow water collections made off Ft. Lauderdale on the southeastern coast of Florida. The only major difference found between the SE Florida specimens and those from further north was the larger size of the former (1 ovigerous female from South Carolina was 6.5 mm). Guțu (2006) reported this species off Carrie Bow Cay, Belize which extended its range into the northwestern Caribbean Sea. Examination of material from MAFLA also revealed the presence of *M. bahamensis* at a depth of 50 m, which extends its range into the GOM.

This species can be distinguished from its congeners by its distinct armature of the female cheliped (Figure 5B) and the absence of anterolateral apophyses on the pereonites (Figure 5A).

*MESOKALLIAPSEUDES BRASILIENSIS* (BĂCESCU, 1986) (Figure 7)



**Figure 7.** *Mesokalliapseudes cf. brasiliensis* (MZUSP 16.899). A. Dorsal view of body. Scale bar = 1.0 mm. B. Spiniform seta of mandibular palp. Scale bar = 0.05 mm. C. Cheliped. Scale bar = 0.2 mm.

*Kalliapseudes viridis brasiliensis*: Băcescu 1986: 93, 95, 96, figure 2.

*Kalliapseudes (Mesokalliapseudes) viridis brasiliensis*: Guțu 2006: 142.

*Mesokalliapseudes brasiliensis*: Guțu 2006: 142; Drumm and Heard 2007: 459, 467.

**Type material:** Holotype female (MHN Grigore Antipa No. 695).

**Material examined:** 7 adult males, 9 females with oostegites and 4 ovigerous females (MZUSP 16.899), Brazil, 23°36'S, 44°46'W, 48 m depth; 5 females with oostegites (1 partly dissected), 3 females with emptied marsupium, 5 adult males (1 partly dissected), Trinidad, sta. 5–1, coll. August 2003.

**Diagnosis:** Rostrum round, tapering anteriorly. Pereonites lacking anterolateral apophyses. Pleotelson broader than long. Inner flagellum of antennule with three articles; first peduncle article about 3.3 times as long as broad. Third article of antenna without distinctive spinulate process. Terminal spiniform seta of mandibular palp naked and stout, approximately seven times as long as broad. Fixed finger of the propodus of cheliped less than one half the length of dactylus. Cutting edge of the dactylus of cheliped with 3 or 4 setae midway and one distal seta near unguis. Pereopod 6 dactylus with one subterminal seta. Last article of uropod exopodite approximately 1.6 times as long as second article.

**Type locality:** East of Port of Tubarão, Brazil, 20°15.5'S, 40°05.3'W, 29 m depth (Figure 8).

**Geographic distribution:** SW Atlantic (Brazil) and NW Atlantic (Trinidad), bathymetric range: 29–48 m (Figure 8).

**Remarks:** Examination of new material extends the range of this species in the northwest Atlantic off Trinidad. *Mesokalliapseudes brasiliensis* was originally considered a subspecies of *M. viridis* (Băcescu 1986); subsequently, Guțu (2006) considered it a valid species based on the different geographical distributions of the species but recognized the very scant original description. Băcescu (1986) described this species as lacking lateral plumose setae on the pleonites, but Guțu (pers. comm., Bucharest “Grigore Antipa” Natural History Museum, Romania) examined the type material and confirmed the presence of plumose setae. Guțu (pers. comm.) compared the type specimen to our illustrations and noted only 2 differences: 1) the number of ventral spiniform setae on the pereopod 1 propodus (3 in our specimen and 2 in the type specimen) and 2) the number of spiniform setae on the pereopod 6 dactylus (2 or 3 in our specimens and 4 in the type specimen). These characters have been shown to vary within species (one ovigerous female we examined had 4 spiniform setae on the pereopod 6 propodus) so they should not be used to diagnose species. One of the most important characters for distinguishing species of *Mesokalliapseudes* is the nature of the cheliped (i.e., setation/spination on the cutting edges and the proportion of dactylus/propodus fixed finger length). The specimens we examined have 3 or 4 setae midway on the cutting edge of the dactylus and one seta distally near the unguis (Figure 7C). Guțu (pers. comm.) examined the type specimen cheliped and did not notice any setae on the cutting edge, but mentioned that this could be due to poor preservation. We have decided to treat this species as conspecific with *M. cf. brasiliensis sensu stricto* rather than give it designation as a new species until further material (topotypic) can be examined.

*MESOKALLIAPSEUDES SONIADAWNAE* BAMBER, 1993 (Figure 14F)

*Kalliapseudes (Mesokalliapseudes) soniadawnae* Bamber 1993: 122, figures 1–4; Drumm 2003: 2, 11; Guțu 2006: 141.

*Kalliapseudes soniadawnae*: Bamber 1993: 128, 129, 130.

*Mesokalliapseudes soniadawnae*: Guțu 2006: 142, 151.

**Type material:** Holotype female (NMW.Z.1991.099.1), 1 paratype male (NMW.Z.1991.099.2).

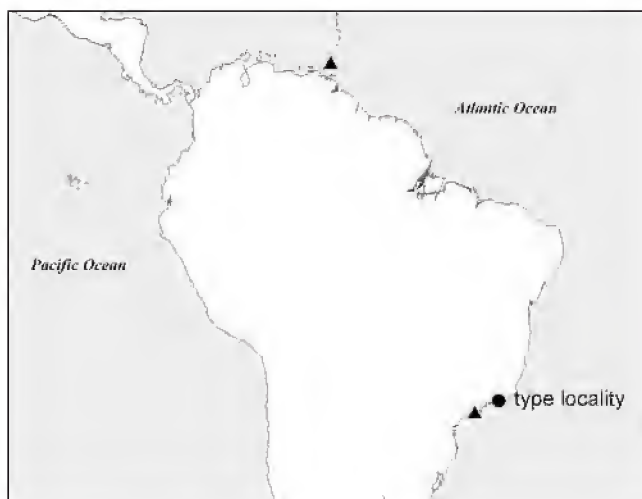
**Material examined:** None available for study.

**Diagnosis** (from Bamber 1993): Rostrum rounded. Anterolateral apophyses on pereonites 2–6. Pleotelson broader than long. Inner flagellum of antennule with three articles. Third peduncle article of antenna not spinulate. Mandibular palp terminally with long seta. Fixed finger of propodus of cheliped less than one half length of dactylus.

**Type locality:** Caribbean Sea, Trinidad, 10°40'N, 61°35'W, depth 10 m.

**Geographic distribution:** Known only from the type locality.





**Figure 8.** Map showing the distribution of *Mesokalliapseudes* cf. *brasiliensis*. The black circle represents the previously published record and triangles indicate new distribution locations.

**Remarks:** Attempts to borrow type material from the National Museum of Wales were unsuccessful. Based on Bamber's (1993) description, this species can be distinguished from the other congeners by the following characters: 1) a short stout pectinate spiniform seta on the ventrodistal corner of the pereopod 1 basis, and 2) no spinulate process on the second peduncular article of the antenna.

*MESOKALLIAPSEUDES THALASISPELEUS* GUȚU, 2006 (Figures 14H, J)

*Mesokalliapseudes thalasispeleus* Guțu 2006: 142–151, figures 209–231.

**Type material:** Holotype female with oostegites no. 250.299, 1 allotype male no. 250.300, MHN Grigore Antipa.

**Material examined:** None available for study.

**Diagnosis** (from Guțu 2006): Rostrum rounded. Pereonites lacking anterolateral apophyses. Pleotelson as long as broad. Inner flagellum of antennule with three articles. Third peduncle article of antenna not spinulate. Mandibular palp terminally with short spiniform seta. Fixed finger of propodus of cheliped less than one half the length of dactylus. Female cheliped with less than 10 short spiniform setae on dactylus cutting edge.

**Type locality:** NW Atlantic, Exuma Cays, Bahamas, approximate coordinates: 23°32'N, 75°50'W (exact coordinates unknown).

**Geographic distribution:** Known only from the type locality.

**Remarks:** *Mesokalliapseudes thalasispeleus* is the second known species of *Mesokalliapseudes* identified from the Bahamas, the other one being *M. bahamensis* and can be distinguished from it and the other congeners by two major characters: 1) the shape of the pleotelson (as long as broad; all other species are broader than long), and 2) the short spiniform seta on the mandibular palp terminus. *Mesokalliapseudes thalasispeleus* appears to be unique in having lon-

ger than usual simple setae on the anterior and posterior corners of the pereonites (approximately as long as the associated pereonite).

SUBFAMILY TANAPSEUDINAE BĂCESCU, 1978

GENUS *PSAMMOKALLIAPSEUDES* LANG, 1956

**Diagnosis:** Antennule inner flagellum not reduced. Cheliped and pereopod 1 with exopodite.

*PSAMMOKALLIAPSEUDES GRANULOSUS* BRUM, 1973 (Figures 9, 13E)

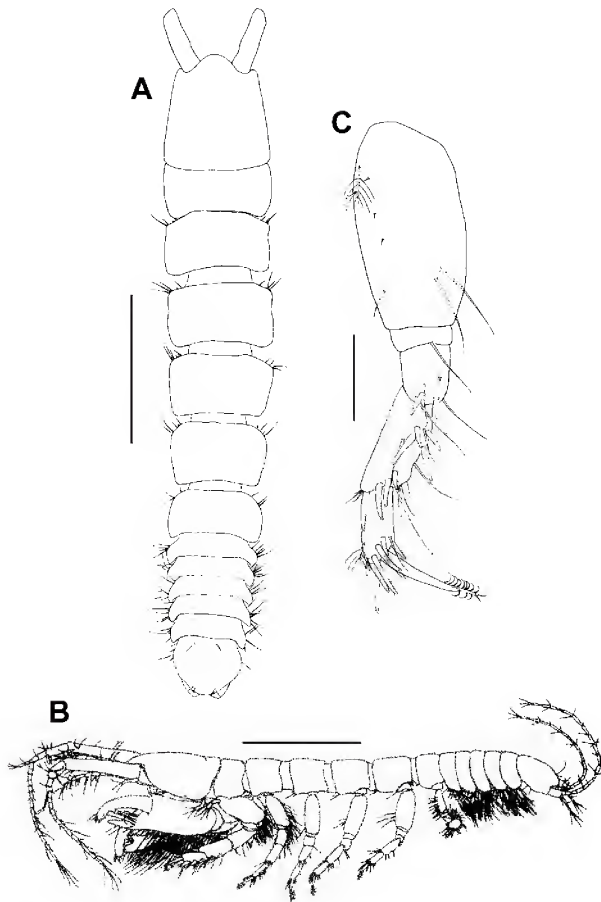
*Psammokalliapseudes granulatus* Brum 1973: 2–3, figure 2; 1974: 4–7, figures 8–26; Băcescu 1979: 3; Băcescu and Absalão 1985: 53.

*Cirratodactylus floridensis* Gardiner 1973: 237, figures 1–6; Băcescu and Absalão 1985: 53; Sieg 1986: 22; Guțu 1996: 70.

**Type material:** None apparently by original designation.

**Material examined:** 3 subadult males (USNM 1011363), ~ 2.9 mm, Ft. Lauderdale, FL, 25°59'14"N, 80°05'25"W, 20 m depth, coll. June 1992, det. David Drumm; 1 female with oostegites (USNM 141481), North Miami, FL, 25°54.7'N, 80°06'W, 15 m depth, sand, coll. May 1964; 2 spec., MAFLA station 2103, 26°25'N, 83°57'W, 33 m, fine sand, coll. 1976, det. Heard and Sieg 1983; 4 spec., MAFLA station 2104, 26°25'N, 83°23'W, 53 m, coarse sand, coll. 1975, det. Heard and Sieg 1983; 2 spec., MAFLA station 2211, 27°56'N, 83°52'W, 43 m, coarse sand, coll. 1975, det. Sieg and Heard 1983; 2 spec., MAFLA station 2315, 28°33'N, 84°20'W, 38 m, silty fine sand, coll. 1975, det. Heard and Sieg 1983; 3 spec., MAFLA station 2317, 28°56'N, 84°05'W, 29 m, silty, very fine sand, coll. 1975, det. Heard and Sieg 1983; 2 spec., MAFLA station 2422, 29°30'N, 84°27'W, 24 m, medium fine sand, coll. 1976, det. Heard and Sieg 1983; 2 spec., MAFLA station 2424, 29°13'N, 85°00'W, 27 m, medium sand, coll. 1975, det. Heard and Sieg 1983; 23 spec., MAFLA station 2425, 29°05'N, 85°15'W, 36 m, medium sand, coll. 1975, det. Heard and Sieg 1983; 3 spec., MAFLA station 2426, 28°57'N, 85°23'W, 82 m, fine sand, coll. 1977, det. Heard and Sieg 1983; 3 spec., MAFLA station 2528, 29°54'N, 86°04'W, 37 m, coarse sand, coll. 1975, det. Heard and Sieg 1983; 3 spec., MAFLA station 2529, 29°55'N, 86°06'W, 38 m, coarse sand, coll. 1975, det. Heard and Sieg 1983; 10 spec., MAFLA station 2530, 29°51'N, 86°06'W, 41 m, medium sand, coll. 1976, det. Heard and Sieg 1983; 2 spec., MAFLA station 2532, 29°46'N, 86°12'W, 45 m, coarse sand, coll. 1975, det. Heard and Sieg 1983; 2 spec., MAFLA station 2748, 27°37'N, 83°53'W, 50 m, coarse sand, coll. 1976, det. Heard and Sieg 1983; 2 spec., MAFLA station 2853, 29°18'N, 84°19'W, 29 m, coarse sand, coll. 1977, det. Heard and Sieg 1983; ~35 specimens (adult males, females, juveniles, manca), Culebra Island, Puerto Rico, 28 m, coll. 2003; 1 adult female, Lover's Beach, northeastern edge of Man-O-War Bay, Tobago, 11°18'15"N, 60°31'25"W, April





**Figure 9.** *Psammokalliapseudes granulosus* from Puerto Rico. A. Dorsal view of body of adult female with oostegites. Scale bar = 1.0 mm. B. Lateral view of adult male. Scale bar = 1.0 mm. C. Pereopod 5 of adult female. Scale bar = 0.2 mm.

1992, coll. & id. Richard Heard, 2 m depth, coral sand/rubble.

**Diagnosis (adult):** Rostrum rounded. Pleotelson broader than long. Antennule inner flagellum with two articles. Pereopod 1 dactylus with three ventral teeth associated with a short spinule. Dactylus of pereopods 1–6 with distal recurved sensory setae.

**Type locality:** Ponta dos Calderos e a Ilha Redonda, Brazil (Figure 10).

**Geographic Distribution:** Brazil, Caribbean Sea (Puerto Rico, Tobago), NW Atlantic (South Florida), eastern GOM, bathymetric range: 20–82 m (Figure 10).

**Remarks:** *Psammokalliapseudes granulosus*, originally described from Brazil, was reported as a new genus and species, *Cirratodactylus floridensis* by Gardiner (1973) a few months later from South Florida waters. Gardiner (1973) further designated a new monotypic family Cirratodactylidae Gardiner, 1973 to accommodate it. Băcescu and Absalão (1985) synonymized *C. floridensis* with *P. granulosus*, relegating the genus *Cirratodactylus* and family Cirratodactylidae to junior synonyms of *Psammokalliapseudes* Lang, 1956 and Kalliapseudidae, respectively.

Examination of new material and MAFLA material ex-

tends this species range into the Caribbean Sea (Puerto Rico and Tobago) and the eastern GOM and its depth range is extended to 82 m. This species can easily be distinguished from its only other congener *P. mirabilis* and is unique among tanaidaceans in having curled sensory setae on the dactylus of all of the pereopods (Figure 9C). Examination of manca (postembryological instars with incompletely developed postcephalic appendages) revealed the presence of exopodites on the last two pereopods. This represents the first record of this occurring in the genus *Psammokalliapseudes*.

#### GENUS TANAPSEUDES BĂCESCU, 1978

**Diagnosis:** Antennule inner flagellum reduced. Cheliped and pereopod 1 lacking exopodite.

*TANAPSEUDES GUTUI* HANSKNECHT, HEARD AND BAMBER, 2002 (Figures 11, 13F, G).

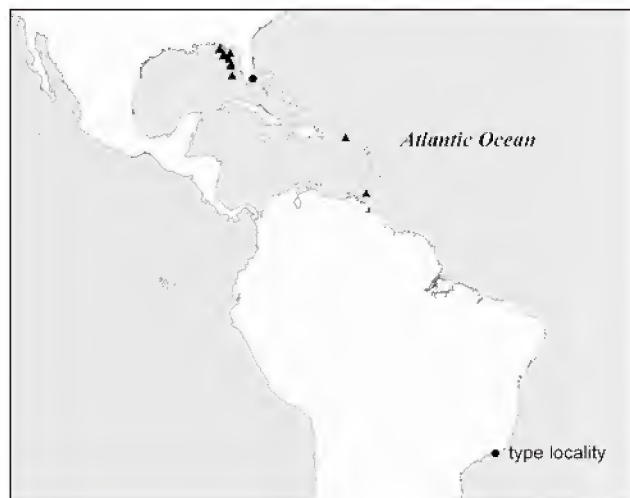
*Tanapseudes gutui* Hansknecht et al. 2002: 67, figures 1–2.

**Type material:** Holotype: adult male (USNM 1001787).

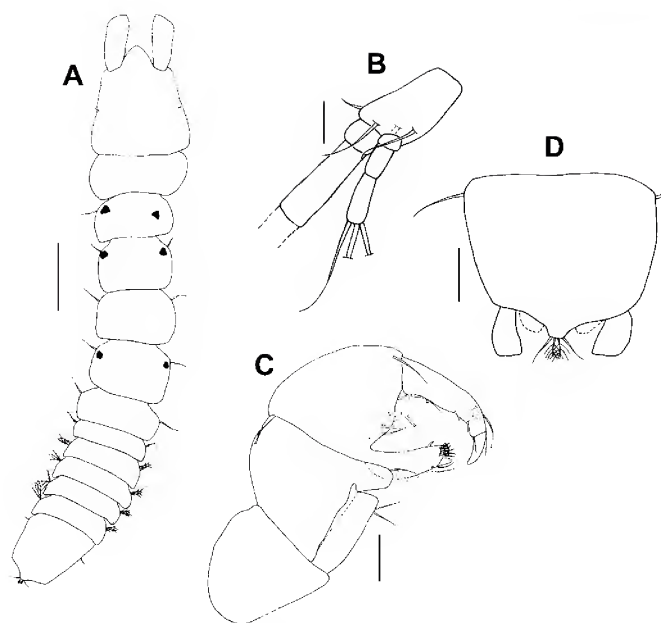
**Paratypes:** 2 males, 1 ovigerous female (USNM 1001788); 1 male, 1 ovigerous female (GCRL 2038); 1 male (MHN Grigore Antipa No. 250.181); 2 ovigerous females (MHN Grigore Antipa No. 250.180); 1 male (NHM 2001.6903); 1 female (NHM 2001.6904).

**Material examined:** Paratypes: 1 ovigerous female, 1 adult male, GCRL 2038, CH2MHill Consultants, Carolina WWTP, Puerto Rico, San Juan Estuary, 18°27.80'N, 65°53.44'W, St. CI-2, 34 m, sandy clay, 30 October 1999. Non-types: 1 adult male, EPA Coastal 2000, 6701, St. PR44, Puerto Rico, id. Tom Hansknecht; 3 males, 1 female and 2 juveniles, MAFLA station 2426, 28°57'N, 85°23'W, 82 m, fine sand, coll. 1977.

**Diagnosis:** Pleonites with only few (3 at most) lateral plumose setae. Pleotelson with very pronounced rounded posterior protuberance. Male pereopod 1 with dorsodistal spiniform



**Figure 10.** Map showing the distribution of *Psammokalliapseudes granulosus*. Black circles represent previously published records and triangles indicate new distribution locations.



**Figure 11.** *Tanapseudes gutui*, adult male. A. Dorsal view of body. Scale bar = 0.3 mm. B. Uropod. Scale bar = 0.05 mm. C. Cheliped. Scale bar = 0.01 mm. D. Pleotelson. Scale bar = 0.1 mm.

seta on propodus reduced or lacking. Male cheliped carpus with ventrodiscal rounded protuberance. Pereopods 2–5 with ventral margins of merus and carpus heavily setose. Uropod basal article lacking inner distal spiniform projection.

*Type locality:* San Juan, Puerto Rico, 18°27.80'N, 65°53.44'W, 3–34 m depth (Figure 12).

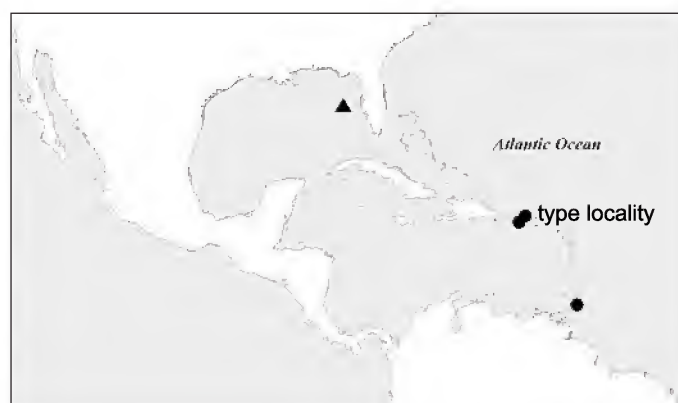
*Geographic distribution:* Caribbean Sea (Puerto Rico, Tobago) and eastern GOM, bathymetric range: 3–82 m depth (Figure 12).

*Remarks:* Examination of MAFLA material extends this species range into the eastern GOM and its depth range is extended to 82 m. Hansknecht et al. (2002) described and illustrated the uropod exopodite of *T. gutui* as being biarticulate. However, examination of type material revealed the presence of 3 articles (1 small round basal article, Figure 11B). They also mention that the adult male cheliped has a tooth midway on the cutting edge of the dactylus; we did not see this tooth on the paratype male we examined (Figure 11C).

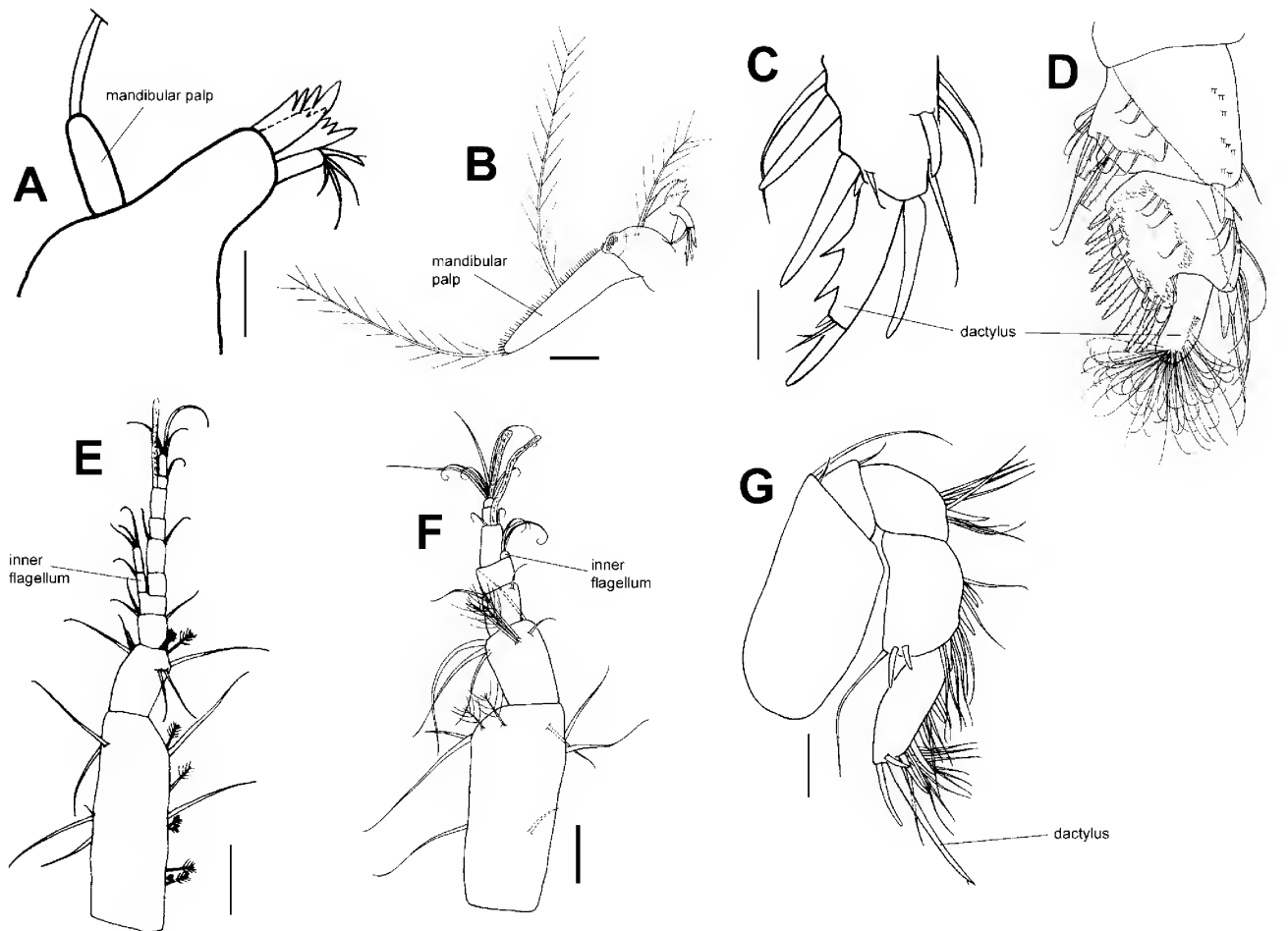
*Tanapseudes gutui* can be distinguished from the other congeners by the male pereopod 1 propodus, which has a reduced dorsodistal spiniform seta and the male cheliped, which has a carpal process (Figure 11C). Guțu and Angsupanich (2005) describe this pattern in specimens collected from the Andaman Sea in Thailand which they attribute to *T. ormuzana*. Their specimens likely represent a new species because these characteristics were not evident in the material examined by us, Hansknecht et al. (2002) or in the original description (Băcescu 1978). The location of their material (Thailand) is also distant from the type locality (Puerto Rico). The posterior protuberance of the pleotelson (Figure 11D) of *T. gutui* also seems to be more pronounced and pereopods 2–5 more setose than in the other species.

## Key to genera and species of Kalliapseudidae presently known in the northwest Atlantic

1. Mandibular palp uniarticulate and short, with one terminal seta (Figure 13A) ..... 2  
Mandibular palp uniarticulate and long, with a row of long, plumose setae (Figure 13B) ..... 3
2. Pereopods with dactylus having curled sensory setae at tip (Figure 9C); antennule with inner flagellum biarticulate (Figure 13E) .....  
..... *Psammokalliapseudes granulosus* Brum, 1973  
Pereopods with dactylus lacking curled sensory setae at tip (Figures 13C, G); antennule with inner flagellum vestigial, uniarticulate (Figure 13F) .....  
..... *Tanapseudes gutui* Hansknecht, Heard and Bamber, 2002
3. Chelipeds not sexually dimorphic; antenna with third peduncle article lacking large triangular tooth (Figure 14C) ..... 4  
.....  
Chelipeds showing strong to moderate sexual dimorphism; antenna with third peduncle article having large triangular tooth (Figure 14D) .....  
..... *Alokalliapseudes macsweenyi* (Drumm, 2003)
4. Pereonites lacking apophyses (Figure 14E) ..... 5  
Pereonites 2–4 with anterolateral apophyses (Figure 14F) .....  
..... *Mesokalliapseudes soniadaunae* Bamber, 1993
5. Mandibular palp armed distally with single spiniform seta (more than 6 times as long as broad) spiniform seta (Figure 7B) .....  
..... *Mesokalliapseudes brasiliensis* (Băcescu, 1986)
- Mandibular palp armed distally with either a single long seta or a single short spiniform seta (less than 6 times as long as broad) spiniform seta ..... 6
6. Pleotelson broader than long (Figure 14G); mandibular palp armed distally with a long simple seta (Figure 14I) .....  
..... *Mesokalliapseudes bahamensis* Sieg, 1982  
Pleotelson as broad as long (Figure 14H); mandibular palp armed distally with a short spiniform seta (Figure 14J) .....  
..... *Mesokalliapseudes thalaspispeus* Guțu, 2006



**Figure 12.** Map showing the distribution of *Tanapseudes gutui*. Black circles represent previously published records and the triangle indicates a new distribution location.



**Figure 13.** Plate 1 for the illustrated key to the NW Atlantic kalliapseudids. A. *Tanapseudes ormuzana*, left mandible. Scale bar = 0.03 mm. B. *Kalliapseudes magnus*, left mandible. Scale bar = 0.1 mm. C. *T. ormuzana*, distal end of pereopod 1. Scale bar = 0.05 mm. D. *Kalliapseudes mauritanicus*, distal end of pereopod 1. Scale bar = 0.1 mm. E. *Psammokalliapseudes granulatus*, antennule. Scale bar = 0.1 mm. F. *Tanapseudes gutui*, antennule. Scale bar = 0.05 mm. G. *T. gutui*, pereopod 3. Scale bar = 0.05 mm.

### Family Characteristics

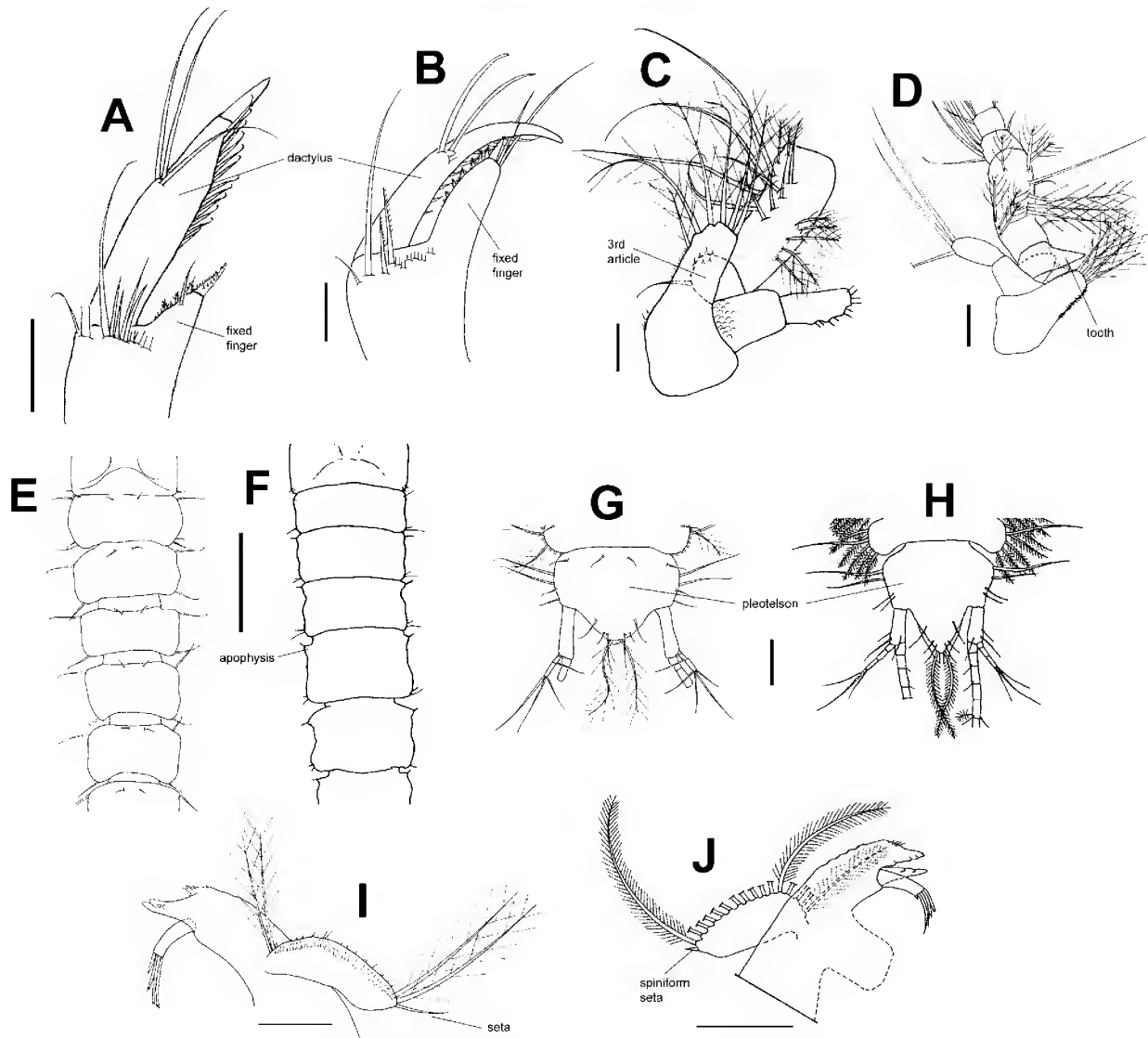
The family Kalliapseudidae is currently defined by the combination of the absence of a palp on the maxillule and the presence of sensory setae on the dactylus of the pereopods. The presence of exopods on pereopods 4 and 5 of the manca (one or more postembryological instars with incompletely developed postcephalic appendages) might be another synapomorphy of the family. The senior author recently confirmed the presence of this character in a species of *Hemikalliapseudes*, constituting the first report of this occurring in the Hemikalliapseudinae. The only exception is the report of the apparent lack of exopodites for the manca stage of *Psammokalliapseudes mirabilis* (Lang 1956). Lang's (1956) observations need further confirmation, since exopods have been reported for all other known mancas for the 3 subfamilies. The only other group of tanaidaceans reported to exhibit this character are members of the sphyrapoid subfamily Pseudosphyrapodinae Guțu, 1980 (see Guțu 2006), a mostly deep-water group with apseudid affinities and not closely related to the Kalliapseudidae. For undetermined reasons, the presence of exopods appear to have been independently retained within these 2 disparate groups.

The sensory setae on the dactylus of the pereopods is a very confusing character and we do not think it should be included in the family's diagnosis or in phylogenetic studies. It is only through theories of homology that phylogenetic analysis can proceed. Position (similarity of topographical relationships) is one key assumption of homology. Some kalliapseudids have terminal sensory setae and some have sub-terminal setae. The structures the setae are attached to are likewise suspect. Members of the Kalliapseudinae definitely have a unique structure: numerous setae attached to a short and thick dactylus. The lack of positional and structural similarities across the subfamilies violates the assumption of homology. The presence of sensory setae on the dactylus of the pereopods is found in the parapseudid genus *Thaïcungella* (Guțu and Angsupanich 2004) and resembles the setae found in some species of the kalliapseudid subfamily Hemikalliapseudinae, so this character should be used with caution.

### Ecology

Little is known of the biology and ecology of most members of Kalliapseudidae. The feeding behavior of two spe-





**Figure 14.** Plate 2 for the illustrated key to the NW Atlantic kalliapseudids. A. *Mesokalliapseudes bahamensis*, female cheliped. Scale bar = 0.1 mm. B. *Alokalliapseudes macsweenyi*, female cheliped. Scale bar = 0.2 mm. C. *M. bahamensis*, antenna peduncle. Scale bar = 0.05 mm. D. *A. macsweenyi*, antenna peduncle. Scale bar = 0.05 mm. E. *A. macsweenyi*, pereonites. Scale bar = 0.5 mm. F. *Mesokalliapseudes soniadaunae*, pereonites modified after Bamber (1993). Scale bar = 0.5 mm. G. *M. bahamensis*, pleotelson. Scale bar = 0.2 mm. H. *Mesokalliapseudes thalaspispeus*, pleotelson modified after Guțu (2006). Scale bar = 0.2 mm. I. *M. bahamensis*, right mandible. Scale bar = 0.1 mm. J. *M. thalaspispeus*, left mandible modified after Guțu (2006). Scale bar = 0.1 mm.

cies [*P. granulosus* (subfamily Tanapseudinae) and *A. macsweenyi* (subfamily Kalliapseudinae)], which distinctly differ in mouthpart morphology, was described by Drumm (2005). Based on the observations of Drumm (2005), *A. macsweenyi* constructs “tubes” in soft sediments using mucus secretions and feeds by filtering detritus and diatoms with plumose setae attached to the chelipeds and maxillipeds. In contrast *P. granulosus*, which lacks a permanent domicile, appears to be fossorial and feeds by scraping the organic material (e.g. microflora) off sand particles (Drumm 2005).

Although a vast majority of the species within the suborder Apseudomorpha are fossorial, (e.g., Apseudidae, Sphyrapidae) or epibenthic (e.g., some Pagurapseudidae and Metapseudidae), some members of the families Kalliapseudidae, Parapseudidae Guțu, 1981, and possibly the

small and poorly known Numbakullidae Guțu and Heard, 2002 appear to occupy permanent or semipermanent tubes or burrow domiciles. Members of the parapseudid genera *Discapseudes* Băcescu and Guțu, 1975 and *Halmyrapseudes* Băcescu and Guțu, 1974 construct well-developed tubes (Băcescu and Guțu 1974, 1975, R. Heard, pers. obser.). However, there can be different interpretations of whether or not members of the subfamily Kalliapseudinae are tube or burrow dwellers, or both. Based on the authors’ personal observations and those of Drumm (2005), we consider *A. macsweenyi* to be a tube dweller *sensu lato*. When the sediments surrounding its vertically oriented domicile are flushed away, a soft mucus “tube” remains; however, it may be a matter of semantics whether this constitutes a true tube or a mucus burrow-lining that remains intact. Members of

the Kalliapseudinae appear to be suspension or filter feeders occupying permanent domiciles in soft-bottom substrata (e.g., sand, sand-silt, mud). In contrast, members of the sub-

families Hemikalliapseudinae and Tanapseudinae, which are also known from soft-bottom habitats, appear to be fossorial deposit feeders that lack permanent domiciles.

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# OBSERVATIONS OF A BLACK GROUPEL (*MYCTEROPERCA BONACI*) SPAWNING AGGREGATION IN BERMUDA

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**ABSTRACT:** Diving observations at a black grouper (*Mycteroperca bonaci*) spawning aggregation site on Bermuda's reef platform revealed many similarities to observations of this species obtained at multi-species spawning aggregation sites in Belize. In addition to similarities in body sizes, color patterns and some behavior, the principal spawning period in the days after the full moon was also similar. Although spawning was not observed in this study, there was ample indirect evidence of spawning at the site, i.e. courtship behavior by males, females with distended abdomens, and color changes. The formation of temporary spawning territories by males and courtship behavior within these territories is described and illustrated. Taken together, these data appear to indicate that the behavior of black grouper at spawning aggregations is consistent across a broad latitudinal range from Belize in the south to the northern limit of the species' range in Bermuda.

## INTRODUCTION

Relatively few studies have been published on the biology of black grouper (*Mycteroperca bonaci*), and most of these studies have concentrated on the reproductive biology of this protogynous hermaphroditic species (Crabtree and Bullock 1998, García-Cagide et al. 2001, Brulé et al. 2003, Teixeira et al. 2004). Spawning seasonality of black grouper at spawning aggregation sites in Cuba has been described by Claro and Lindeman (2003). Although the black grouper is recognized as a transient aggregation spawner (Domeier and Colin 1997), only a small number of studies have described the behavior of this species at fish spawning aggregation sites (FSAS) with the majority of the research being conducted in Belize (Heyman and Kjerfve 2008, Paz and Sedberry 2008). One study in Florida (Eklund et al. 2000) examined an aggregation site in relation to a Marine Protected Area (MPA) boundary but provided less behavioral information as spawning was not observed. Whaylen et al. (2004) reported seeing small groups of black grouper with distended abdomens during observations at a primary Nassau grouper (*Epinephelus striatus*) spawning aggregation site in Little Cayman but spawning was not observed.

Black grouper have been an important species to the Bermuda fishery for decades but suffered a significant decline in landings from the mid-1970s along with many other grouper species (Luckhurst 1996). Although it was known that black grouper aggregated to spawn, the location of spawning sites was apparently not well known in the local fishing industry. In contrast, red hind (*Epinephelus guttatus*) spawning aggregation sites were well-known and heavily fished, which prompted early management action to seasonally protect these sites (Luckhurst 1998, Luckhurst and Trott 2009). In the summer of 2003, the location of a spawning aggregation site for black grouper was revealed by fishermen and this led to research to define the dynamics of the aggregation. It was determined that the black grouper site was relatively close to an exist-

ing red hind site which was seasonally closed to all fishing. Anecdotal evidence indicated that the black grouper site was being heavily fished and that the bag limit of one fish per boat per day was being routinely exceeded. As enforcement of the bag limit was problematic due to the large number of landing sites, it was decided to incorporate the black grouper site into a redefined and enlarged seasonally protected area (Fisheries Protected Areas Order 2004) which included the original red hind spawning aggregation site (Luckhurst, pers. obs.). Only after the site was seasonally closed to fishing was it possible to conduct an intensive research program to study the aggregation and learn more about its dynamics without interaction with fishermen at the site. The data presented here are the first to be derived from this ongoing study.

## MATERIALS AND METHODS

A week before diving observations began, 2 mooring buoys were placed about 40 m apart near the presumed center of the spawning aggregation site at a depth of about 30 m. This was done to avoid anchoring on the site which could have disturbed the aggregated fish and also increased the efficiency of boat operations. There were 2 dive boats on the site for 3 days of the project with a single boat on the remaining 2 days.

Diving observations commenced on the day of the full moon in June 2005 and continued for 6 consecutive days. No diving was possible on the fifth day due to rough sea conditions at the site. Teams of divers from each boat (2-4 divers per team) recorded their observations on waterproof paper on slates and all of the daily observations made during the study were collated and used for the present analysis. Divers surveyed the area widely and made estimate counts of the number of fish within their view and also estimated fish sizes. In addition, divers made notes on behavior and color patterns. After each dive, team members discussed

**TABLE 1.** Summary of daily observations at a black grouper spawning aggregation site in Bermuda in June and August 2005. No observations were made in July. See Figure 3 for further details of the behavior noted on June 26 and August 25. Sunset was at 2030 hrs during the June observation period and at 1954 hrs during the August period.

Date 2005	Time (h)	Moon phase	Fish abundance estimate	Size-FL cm Mean (range)	Observations
June 21	1300	Full	20+	125 (110-150)	Fish hovering mainly over sand holes
	1500		25-30	125 (110-150)	Few color changes but no interactions between fish
	1700		30+	110 (90-150)	Cone-shaped school of 30+ fish hovering above substrate, inactive; pale-body phase fish increasing in number
June 22	1300	Full+1	70-100	No size estimates available	Single layer school moving over substrate, several females with distended abdomens
	1700		200-400	110 (80-150)	Band of fish hovering 7-9 m above reef (10-15 fish high) – 2-4 % of fish in pale-body phase
June 23	1730	Full+2	100-200	110 (100-150)	70-80 % pale-phase fish, band of fish hovering 3-5 m above reef
June 24	1500	Full+3	150-200	100 (90-150)	Band of fish hovering 7-9 m above reef, % of females appears to have increased from June 23
	1815		150+	90 (80-130)	Increased % of females, minimum of 5-6 females with distended abdomens; male courtship observed
June 25		Full+4			No diving – rough sea conditions
June 26	1645	Full+5	150+	90 (80-140)	Males with pale sub-caudal fin margins, females with distended abdomens common, females comprise 90% of fish present, fish becoming more active
	1855		250-300	90 (80-140)	Males (125-140 cm FL) in “sunburst” coloration set up temporary spawning territories, periodically swim 9-12 m. up into water column in courtship behavior, no interaction with females
	1910		250-300	90 (80-150)	Minimum of 12 contiguous spawning territories established, occupied by largest males, all in “sunburst” coloration exhibiting courtship behavior; dark-phase females appear to be sheltering in reef substrate
	1925				Fish were becoming more active at the time that observations ceased
August 24	1300	Full+5	125-150	100 (90-140)	Fish formed cone-shaped school and hovered over reef, 10% pale-phase fish
	1600		150-175	90 (80-140)	Increase in school size, school moving between sand and reef, with associated color changes which were frequent and rapid
August 25	1900	Full+6	125+	(90-150)	Several males observed in “sunburst” coloration in courtship behavior, females largely remain in dark-body phase close to substrate

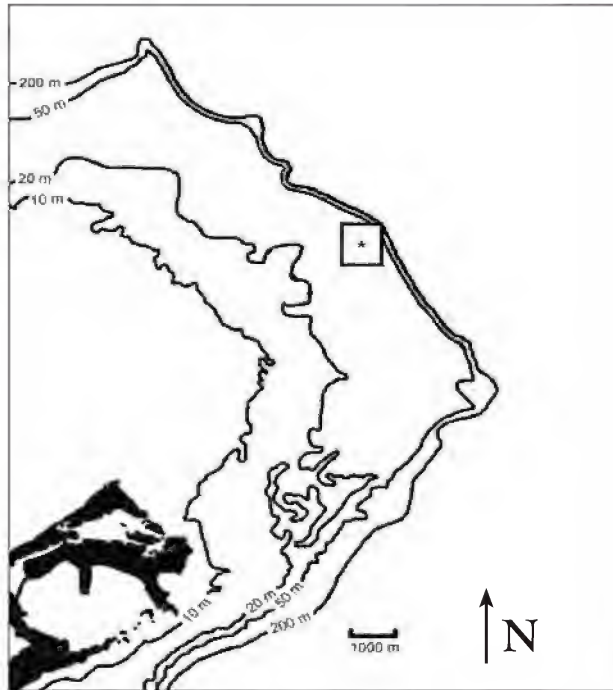
their estimates of numbers and sizes as well as behavioral observations in an attempt to reach a consensus on what had been observed. A videographer roamed the area and captured footage of behavior and color changes. A portion of this footage was subsequently analyzed to confirm and refine divers' observations.

Due to logistical and safety constraints arising from working offshore, the dive teams were not able to remain on site until sundown. This is reflected in the timing of the observa-

tions in relation to sunset (Table 1). Another set of observations was made on the site for 2 days in August 2005, starting 5 days after the full moon. Only 4 divers were involved in these observations.

During observations, males were readily identified due to their larger size (all fish >120 cm fork length (FL)) and were counted as males since earlier research had determined the transition size range from female to male to be 110–120 cm FL (Luckhurst and Trott, unpublished data). Following this





**Figure 1.** Location of black grouper spawning aggregation site on the northeast reef platform of Bermuda. The square (1000 m x 1000 m) is the approximate area within which black grouper were observed during diving observations and the star symbol is the site with the highest observed density of black groupers during diving observations.

protocol, all fishes estimated to be < 120 cm FL were counted as females. Although this species is capable of rapid and dramatic color changes, there was also some consistency in the appearance of the two sexes with smaller females generally being in dark-phase coloration or the normal species color pattern. The interpretation of the pale body coloration is still to be determined but Paz and Sedberry (2008) report that it is seen in both sexes. The width of the sub-marginal black bands of fin pigmentation on the caudal, anal and pectoral fins is also a useful indicator of the sex of the fish (Crabtree and Bullock 1998). In males, these bands are wider and a more intense black. This contrast is accentuated during spawning times, particularly in the caudal fin of males (with a pale caudal margin). Additionally, males in courtship display show a distinctive color pattern on the head. This coloration, termed a “sunburst” pattern by Heyman and Kjerfve (2008) is described and illustrated (Figure 3C in their paper). The same coloration pattern is termed a “white-head” phase male by Paz and Sedberry (2008, Figure 3D). I use the term “sunburst” in this paper as the more descriptive term to describe this pattern in courting males as well as to use a term which is already in the published literature.

## RESULTS

### Site description

The spawning aggregation site was located about 10 km

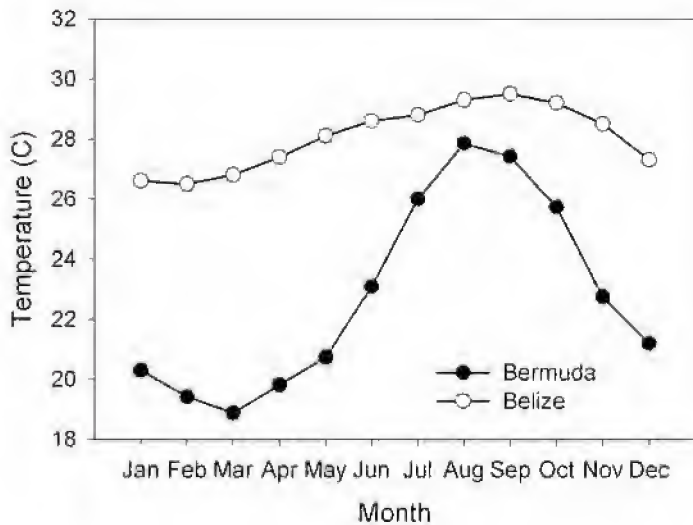
offshore on the northeast reef platform of Bermuda (Figure 1) at a depth of about 30 m. The aggregation area is characterized by an extensive substrate of hard bottom with gorgonians and scleractinian corals. The hard bottom is interspersed with sand holes of variable size, often with ridges between them. The depth in the sand holes is about 33 m while the tops of the ridges range from 24–28 m depth. The bottom gently slopes seaward towards the edge of the reef platform with the shelf break at about 55 m depth. The center of the black grouper site is located about 500 m from the edge of the reef platform (Figure 1).

During the June observations, the surface water temperature was 25°C, however, there was a thermocline present at a depth of about 20 m. Below the thermocline, the temperature was 22°C. There were no water temperature data available from the site for the August observations but divers did not report detecting a thermocline. A comparison of the mean monthly water temperature between Bermuda and Belize (Figure 2) reveals that maximum temperatures occur at about the same time of year (August – September). There is a difference of < 2°C between the maxima (27.9°C in Bermuda in August; 29.5°C in Belize in September). However, the annual temperature range in Bermuda (18.9–27.9°C) is considerably greater than in Belize (26.5–29.5°C).

### Behavioral observations

Table 1 briefly summarizes the daily observations by divers at the site. One of the notable constraints during the project was the underwater visibility which varied from 15–25 m, coupled with the fact that black grouper are generally wary and do not allow a close approach by divers on open-circuit SCUBA (Eklund et al. 2000, Paz and Sedberry 2008). As a result, this hindered divers’ counts and thus estimates of abundance should be viewed as conservative because it was rarely possible to count all of the fish in the field of view clearly. The abundance estimates are mostly given as a range due to the variability of divers’ counts. Because of the spatial extent of the site, it was not always possible to determine if individual divers were counting the same group of fish.

Observations in June 2005 started on the day of the full moon (June 21) when only 30+ fish were counted at the site. The number of fish showed an increasing trend in the following days to about 300 fish on June 26 (moon full + 5), although there was a credible estimate of 400 fish on June 22 (Table 1). The size range of fishes remained reasonably consistent during the 5 days of observations. Although the data are limited, observations confirmed that although males and females were always present on site, females appeared to increase in number during the afternoon and early evening. A small number of females with distended abdomens (a good indirect indicator of spawning readiness) were first observed on June 22 (moon full + 1) and the number of “ripe” females generally increased until observations ceased (Table 1). On June 26<sup>th</sup> (full moon +5), divers observed the establish-



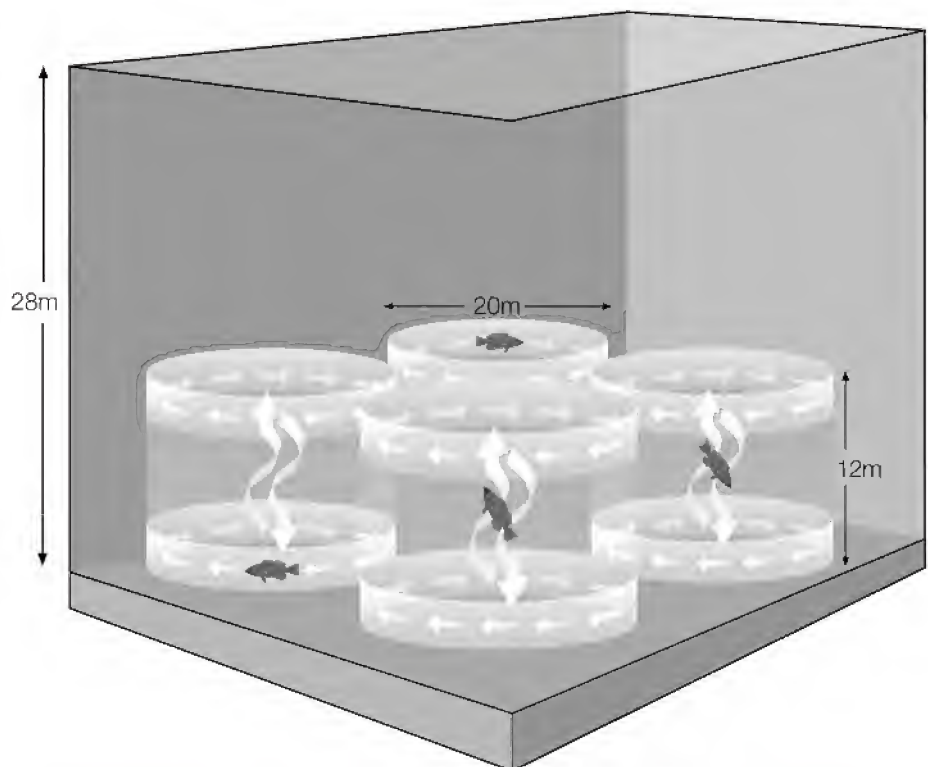
**Figure 2.** Mean monthly water temperature (°C) in Bermuda and Belize. Maximum water temperatures occur during the same period (August – September) but there is greater seasonality in Bermuda than in Belize.

ment of male spawning territories with males in courtship displays showing the distinctive “sunburst” color pattern on the head.

A minimum of 12 male spawning territories were identified by swimming a transect along a ridge line in the late afternoon and counting the large males which were conspicuous swimming above the substrate. These male territories were roughly mapped and appeared to be contiguous. These territories were first observed at 1855 h local time (95 minutes before sunset) but it is not known if they had formed earlier. Divers surveying in the vicinity of these territories during the same time period did not observe any other large males displaying courtship behavior at the site. A diagrammatic representation of male courtship behavior (Figure 3) illustrates the different components of the behavioral sequence. Males began by slowly swimming around the perimeter of their spawning territory about 1–2 m above the substrate. The striking “sunburst” coloration started to become more prominent at this stage. They then turned and swam (in a languid manner) vertically upward in the water column from 9–12 m above the substrate. Upon reaching this height above the substrate, they swam in a circular motion around an imaginary perimeter appearing to delimit their territory as a cylinder (Figure 3). The “sunburst” pattern appeared to become more pronounced when the males were at

the top of the cylinder (J. Pitt, pers. comm., Department of Environmental Protection, Bermuda). After a few minutes, they turned and swam slowly downward to the substrate and apparently resumed the sequence again. No pair spawning rushes or gamete release were observed in this study. However, groups of 6–10 smaller fish in dark-phase coloration (considered to be females) were observed sheltering in the reef infrastructure around the male territories (J. Pitt, pers. comm.) although no interactions with males were detected. Due to the falling light level in the water column, it became increasingly difficult to observe clearly what female behavior was occurring at this time. Interestingly, no other transient spawning species were observed at the site during the five days of observations. It appeared that black grouper dominated the area in terms of both number and biomass.

The observations 2 months later (August 2005) were limited to 5 and 6 d after the full moon (Table 1). With only 4 divers, it was not possible to survey the site as thoroughly as in June but similar schooling behavior by black grouper was observed during the day and color changes were common. The estimate of the number of fish (150–175) present on August 24 (full+5) at 1600 h local time compared with the estimate (150+) on the same lunar day in June at 1645 h is similar (Table 1), but no meaningful conclusion can be drawn from this except to confirm that fish were still present in similar numbers 2 months later. The size range of fish between the 2 periods was also similar (Table 1). Again,



**Figure 3.** Diagrammatic representation of courtship behavior of male black grouper in temporary spawning territories. Measurements given are: 28 m – depth of water, 20 m – diameter of cylinder, 12 m – height above substrate. See text for details of behavior and timing.



there were no observations of other transient spawning species such as groupers or snappers in the area.

Using the limited observational data (Table 1), it is possible to describe a general behavioral pattern of black grouper during the afternoon period at the site. The daily sequence of behavior appears to be the following: 1) Loose schools of fish hover above hard substrate, sometimes forming cone-shaped schools of fish 10–15 layers high, no interactions between fish observed (1300 – 1700 h); 2) The number of females on site increases, fish become more active (1700 – 1800 h); 3) Females with distended abdomens appear more numerous and male courtship behavior is observed (1800 – 1900 h); 4) Males establish temporary spawning territories and commence courtship behavior, females shelter in the substrate in the vicinity of male territories (1900 – 1930 h). These observations were made in the week following the full moon but it is not known for how many days this sequence might continue.

## DISCUSSION

The center of the spawning aggregation site, located about 500 m from the edge of the reef platform (55 m depth), appears to be at a greater distance from the shelf edge than other published descriptions of black grouper spawning aggregation sites. Black grouper aggregations have been found near shelf breaks or at reef promontories in Belize (Heyman and Kjerfve 2008) and Sala et al. (2001) reported that a black grouper spawning aggregation was observed in the vicinity of a series of coral ridges in a spur and groove system close to the shelf break at Glover's Reef, Belize. This site was dominated by Nassau grouper. Whaylen et al. (2004) observed small groups of black grouper at a Nassau grouper spawning aggregation site which is located at a shelf break near a drop-off to deepwater in Little Cayman. Claro and Lindeman (2003) indicated that all of the multi-species spawning aggregation sites which they documented in Cuba were located near the shelf break. However, the black grouper may be more of a generalist as Paz and Sedberry (2008) observed spawning aggregations in a variety of reef formations in Belize. The location of the Bermuda site, at some distance from the shelf break, tends to support this latter observation.

Spawning seasonality in black grouper based on gonad histology has determined that the peak spawning period in populations to the south of Bermuda is from January to March (Florida – Crabtree and Bullock 1998, southern Gulf of Mexico – Brulé et al. 2003). Claro and Lindeman (2003) indicated that the peak of the spawning season for black grouper in Cuba was from February to March around the full moon. Diving observations of spawning seasonality at Gladden Spit, Belize indicate that peak spawning in black grouper occurs during the period January – March from 5–14 d after the full moon (Heyman and Kjerfve 2008). A survey of spawning aggregation sites in Belize revealed that

peak spawning occurred in January – February and that black grouper were most abundant at sites from the full to the last quarter moon (Paz and Sedberry 2008). In summary, all of the black grouper populations at latitudes south of Bermuda have a winter spawning pattern. However, the summer spawning period (June – August) for black grouper in Bermuda is consistent with the spawning periods of other local groupers such as red hind (Luckhurst 1998), coney *Cephalopholis fulva* (Trott 2007) and lane snapper *Lutjanus synagris* (Luckhurst et al. 2000).

Thus, it appears that black grouper spawn at the warmest time of year in Bermuda and at a similar temperature, but at the coldest time of year, further south, e.g. Belize (Figure 2). Paz and Sedberry (2008) recorded a bottom temperature range of 24–27°C in Belize at black grouper spawning aggregation sites. This minimum is lower than that recorded at Gladden Spit by Heyman et al. (2005) but this may simply be the result of oceanographic variations. The bottom water temperature (22°C) observed at the aggregation site in the present study in June was recorded below a thermocline but it is not known whether a thermocline is a consistent feature of the oceanography at this site during this time period. A bottom temperature of 25°C was recorded at a shallower red hind spawning aggregation site in June (Luckhurst 1998) in the vicinity of the black grouper site. Although diving observations ceased 5–6 days after the full moon, strong evidence of an increase in fish abundance (in June) and imminent spawning (courtship and color changes, both June and August) was observed. However, it is not known how long the aggregation remained intact for either observation period or how long spawning may have continued. Heyman and Kjerfve (2008) indicated that the lunar abundance peak of black grouper occurred 5–14 d after the full moon.

The data presented here are broadly similar to the detailed observations made in Belize and appear to confirm consistent behavioral patterns of black grouper in this spawning aggregation at the northern edge of the species range. The number of black grouper observed in aggregations in Belize over several years ranged from 25 to 375 (Paz and Sedberry 2008), a range similar to that reported here (20+ to 400) for a very limited time period. Heyman and Kjerfve (2008) reported a maximum total of about 150 fish at a multi-species aggregation site at Gladden Spit and Sala et al. (2001) reported a similar maximum (140 fish) at Glover's Reef.

Paz and Sedberry (2008) stated that spawning took place at sunset and Heyman and Kjerfve (2008) observed spawning 15–20 min before sunset. As the observations in the present study terminated at least one hour before sunset (Table 1), it is perhaps not surprising that the spawning act (i.e. gamete release) was not observed. Both Paz and Sedberry (2008) and Heyman and Kjerfve (2008) described pair spawning in black grouper but neither described the full male courtship behavioral sequence documented here. Perhaps this is simply a



variation of the basic spawning behavior already described by these authors. Several elements of the behavioral sequence described for Bermuda are similar to those reported for males in “white-head” coloration (Paz and Sedberry 2008); these authors determined that this color pattern was observed only in mature males in spawning condition. Furthermore, this coloration was only seen in males during spawning months (December–March) in Belize (Paz and Sedberry 2008). By extrapolation, the observation of this male color phase in both June and August suggests that these are active spawning months in Bermuda. Although no observations were made in July, it is reasonable to assume that spawning could have occurred in that month, leading to a conclusion of a

minimum spawning period of 3 lunar months in Bermuda. This is consistent with the 3 month peak spawning period at Gladden Spit (January–March) documented by Heyman and Kjerfve (2008). Recent acoustic tagging data collected from the Bermuda site indicates that the aggregation may form monthly for a period of 5–6 months (Trott, Luckhurst and Pitt, unpublished data) but additional data is required to confirm this time period. The important issue of whether spawning is occurring in each aggregation month will require continued monitoring of the site. These data are essential to better define the range and variation of the elements of this aggregation which will allow for more responsive and effective management of this commercially valuable species.

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# EVALUATING MANAGEMENT ACTIONS FOR SPOTTED SEATROUT, *CYNOSCION NEBULOSUS*, IN MISSISSIPPI WITH AN AGE-STRUCTURED PROJECTION MODEL

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**ABSTRACT:** Spotted seatrout, *Cynoscion nebulosus*, is an important recreational fishery in the coastal waters of the Gulf of Mexico and is the most sought after gamefish in coastal Mississippi. The management of *C. nebulosus* is state-specific, and unlike other similarly managed species, data on both population structure and movement support the existence of local sub-stocks. It is important for each state to clearly examine its own sub-stock in the context of its own state fishery in order to properly manage for local sustainability. We used an age-structured assessment model to examine the status (1993–2005) of the Mississippi *C. nebulosus* population and to project forward several probable management actions (i.e., length limits) while also accounting for uncertainty in both fishing mortality and annual recruitment. Model results suggest annual fishing mortality for Mississippi *C. nebulosus* is close to  $F_{msy}$ , but that spawning stock biomass (SSB) is not below  $SSB_{msy}$ . This suggests the sub-stock is currently stable, but with high fishing pressure and a high dependence on annual recruitment to the fishery. Projections suggest that when uncertainty in angler effort and annual recruitment are included in the analysis, more conservative management actions are warranted in order to achieve both higher fishery yield and stable SSB.

## INTRODUCTION

Spotted seatrout, *Cynoscion nebulosus*, is an important recreationally and commercially harvested species in all states bordering the northern Gulf of Mexico (GOM, GSMFC 2001). In particular, the landings of *C. nebulosus* have been increasing in coastal Mississippi state waters since 1995 as spotted seatrout are the dominant target of recreational anglers within the state. While historically the commercial harvest of *C. nebulosus* has been high, recreational landings have represented over 90% of total landings since 1981 (NMFS Fisheries Statistics Section unpublished data). As a result, the recreational management of *C. nebulosus* in Mississippi is a significant issue that receives a lot of public attention.

Although *C. nebulosus* is harvested across the northern GOM coast, there is evidence that there is not a single GOM stock but multiple sub-stocks. *Cynoscion nebulosus* is a non-migratory estuarine-dependent species (Gold and Richardson 1998) that can be found in a variety of coastal habitats, but is generally found in shallow water (< 1 m) associated with rooted vegetation (GSMFC 2001). Data from tagging studies in Mississippi and elsewhere indicate that individual adult fish are highly unlikely to travel more than 15 km both within and between years (Moffett 1961, Baker and Matlock 1993, Hendon et al. 2002). These data support the idea that there are sub-stocks of *C. nebulosus* differentiable at a scale consistent with each GOM state, and it is reasonable to generate both independent stock assessments and management regulations for each GOM state. This is consistent with existing management in that *C. nebulosus* are managed independently within each state as a part of a cooperative agreement between states (GSMFC 2001).

Regulations for the recreational harvest of *C. nebulosus*

vary greatly by GOM state (Table 1). Yet, all five states have adopted a proxy for maximum sustainable yield (MSY) based on the spawning potential ratio (SPR). The SPR measures the reproductive potential of the fished stock in comparison to the reproductive potential of the virgin (i.e., unfished) stock. The SPR proxy can be estimated from age-structured landings data and provides an easily interpretable benchmark against which to determine stock status. Not all states have a target SPR value but all 5 states report the SPR for their state as part of their respective stock assessment.

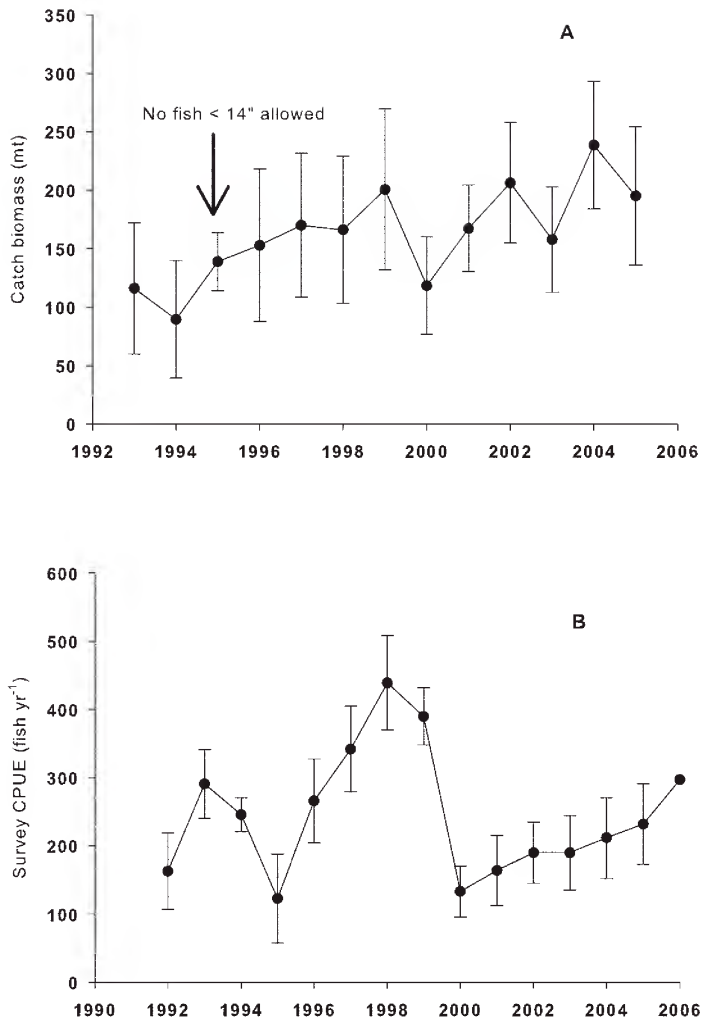
The recreational fishery for *C. nebulosus* in Mississippi is particularly important in comparison to other state-managed fisheries. An analysis of angler interview data for Mississippi indicates that *C. nebulosus* is the dominant target species among anglers in Mississippi (National Marine Fisheries

**TABLE 1.** Current fishery regulations for *Cynoscion nebulosus* by Gulf of Mexico (GOM) state. SPR—spawning potential ratio.

State	Minimum size limit (in)	Daily Bag limit	Target SPR
Florida	15-20*	5	35%
Alabama	14	10	30%
Mississippi	13	15	n/a
Louisiana	12	25	18%
Texas	15-25**	10	30%

\*FL allows 1 fish/day > 20" TL

\*\*TX allows 1 fish/day > 25"



**Figure 1.** Time series of catch for *Cynoscion nebulosus* in Mississippi. A. Female recreational catch. B. Index catch per unit effort (CPUE) from fishery-independent data. Arrow in upper panel indicates only major regulatory change between 1993 and 2005. Error bars are  $\pm 1$  se.

Service Fisheries (NMFS) Statistics Division, pers. comm., Mississippi Department of Marine Resources (MS-DMR, unpublished data). However, Mississippi has not established formal benchmarks for assessment of stock status and while benchmarks have been established in several other states, these benchmarks, and the associated management regulations, should not be applied to assessment of the Mississippi stock without some examination of the projected effect.

Management of *C. nebulosus* in Mississippi has undergone several changes over the last 30 years, but has been relatively stable between 1995 and 2007. Since initial adoption, recreational management regulations have included both a minimum length limit and a daily quota (i.e., bag limit) for harvest. The daily quota has ranged from 10 to 50 but has been set at 15 since 1996. Minimum length limits have ranged from 12" (305 mm) to 14" (356 mm) total length (TL) but were set at 14" from 1995 to 2006. In 2007 the minimum length limit was reduced to 13" (330 mm) TL.

The recent change in the length limit was initially proposed based on public comments that the 14" length limit resulted in a high level of sub-legal catch and release for near-shore anglers (MS-DMR, unpublished public comments). No formal stock assessment of *C. nebulosus* in Mississippi is available to evaluate this change in the management regulations.

Management regulations for recreational fisheries, like those for commercial fisheries, are primarily focused on maximizing harvest and/or angler satisfaction while also maintaining a stable population (Hilborn and Walters 1992). Achieving this dual objective in a recreational fishery is complicated by highly variable effort, highly variable catch per unit effort (CPUE), and low reporting rates for landings. Common management options include setting a maximum CPUE (i.e., daily quotas) combined with length limits to protect spawning stock biomass (SSB) and maintain a target SPR. The influence of either bag limits or minimum length limits on fishing mortality is greatly affected by variability in the rate of recruitment, as well as changes in angler effort through time. Evaluating the appropriateness of management actions under these circumstances can be difficult and involves much uncertainty regarding the effect on long-term population stability.

Quantitative models offer a powerful tool for both the assessment of fishery stocks and the evaluation of potential management decisions (Hilborn and Walters 1992). In particular, statistical catch at age (SCAA) models allow individual cohorts to be tracked through time as a method for estimating total population mortality rate, recruitment, and SSB. Such models also provide a framework for the evaluation of management actions by projecting fishery yield and SSB based on estimated changes in fishing mortality and future recruitment. This approach has been used to establish future status and compare management actions for Atlantic cod (*Gadus morhua*, Reich and DeAlteris 2009), lake whitefish (*Coregonus clupeaformis*, Mohr et al. 2007), and North sea plaice (*Pleuronectes platessa*, Hoff and Frost 2008).

In the case of *C. nebulosus*, SCAA models provide an approach for exploring the relative influence of the range of management regulations applied across the 5 GOM states on the Mississippi stock. This analysis is not therefore a formal assessment of the stock, but rather an exploration of possible management outcomes with a stock assessment model that we hope is a step towards a formal assessment in the future. In this study we applied an SCAA model to examine the Mississippi population of *C. nebulosus* with 3 objectives: (1) to estimate current stock status of the Mississippi population relative to MSY-based benchmarks, (2) to evaluate the range of minimum length limits currently applied to *C. nebulosus* across the GOM in terms of their relative effect on population sustainability in Mississippi, and (3) to explore the effect of changes in future recruitment and angler effort on population sustainability and how

these factors should affect management decisions. The focus on minimum length limits as the primary management tool was based on current discussions regarding management of *C. nebulosus* in Mississippi and the need to understand the influence of length limits on population stability.

## METHODS

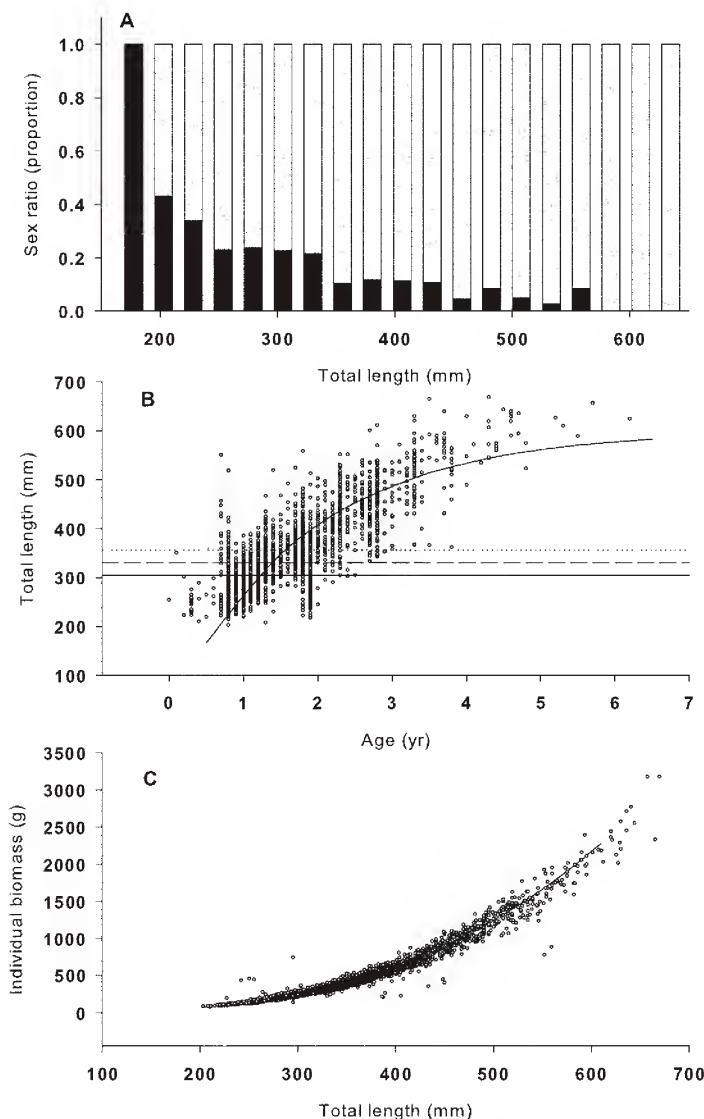
Data used for this model assessment of *C. nebulosus* were a combination of fishery independent and fishery dependent data. Recreational landings (1993–2005) of *C. nebulosus* were estimated from creel data collected in Mississippi as a part of the Marine Recreational Fisheries Statistics Survey (MRFS; NMFS Fisheries Statistics Section unpublished data; Figure 1A). These data included both landings and dead discards as model input. A time series (1993–2005) of fishery independent catch per unit effort (CPUE) was used to constrain the

model and came from a gillnet survey conducted monthly at eight survey sites along the Mississippi Gulf coast (Figure 1B; University of Southern Mississippi – Center for Fisheries Research and Development (CFRD) unpublished data). While there is a commercial harvest of *C. nebulosus* in Mississippi, these landings are small (about 10% of total landing; NMFS Fisheries Statistics unpublished data) and are not affected by recreational management actions. Commercial harvest is almost entirely hook and line with a 14" length limit and a 40,000 lb annual quota since 1986 (MS-DMR, unpublished data). Commercial harvest was included in the model as a separate but constant fishing mortality term.

Length frequency of the catch as reported by MRFSS was converted to age frequency for females only based on estimates of sex ratio at length (Figure 2A) and year-specific age-length keys (ALK) that were both based on *C. nebulosus* collected, sexed, and aged by the University of Southern Mississippi CFRD ( $n = 3,524$ , mean = 244/yr). Model input also included estimates of percent maturity at age for spotted seatrout in Mississippi (Brown-Peterson and Warren 2001, Brown-Peterson et al. 2002). Growth rates of female spotted seatrout in Mississippi were also estimated from size-at-age and biomass-at-age data collected independent of the fishery (Figure 2B, C; 1993–2006, CFRD unpublished data). Natural mortality of spotted seatrout in Mississippi was estimated to be 0.3 for all model simulations based on an analysis of longevity and growth parameters used in previous assessments (GSMFC 2001).

## Model description

The model assessment was conducted using a SCAA Model (ASAP2; NMFS NEFSC Fisheries Toolbox <http://nft.nefsc.noaa.gov/>). The ASAP2 model is a non-linear optimization model that estimates average fishing mortality and spawning stock biomass by age class based on minimization of an objective function that describes model fit to fishery landings, index CPUE, as well as fishery and index age compositions. Nine age classes were included in model simulations (age 0–8) with no plus group. The model fit was constrained both by estimates of variability for each data input source (Table 2) and a Beverton–Holt stock–recruitment function with an initial steepness of 0.6 (Haddon 2001). The initial steepness value was chosen to be neutral, however final steepness was fully estimated by the model and was not strongly influenced by the initial value. Error structure for both fishery landings and index CPUE were assumed to be lognormally distributed while error structure for the age compositions had a multinomial distribution. Effective sample size for the multinomial distribution was set at 200 for all years based on mean annual coverage of the age data used to build the ALK. The ASAP2 model has been used to conduct formal stock assessments of several fish stocks including red grouper, *Epinephelus morio*, and yellow tail flounder, *Pleuronectes ferrugineus*, (Schirripa et al. 1999, Legault et



**Figure 2.** Metrics for *Cynoscion nebulosus* in Mississippi. A. Sex ratio. Black bars are males and grey bars females. B. Total length at age for females. Reference lines indicate cutoff for 12" (—), 13" (---), and 14" (···) length limits. C. Biomass at total length for females. Points in panels B and C are individual fish ( $n = 3,524$ ).



**TABLE 2.** Input parameters for the age-structured model. Initial value is the value input to the model which remained constant if Fixed (F), but could change during the optimization if Estimated (E). Selectivity values for length limits of 12 and 13" were only used to perform model projections.

Parameter	Initial value	F/E	Final value	Model component
Natural mortality	0.3	F	0.3	Estimate non-fishing mortality
Steepness	0.6	E	0.8	Stock-recruitment curve
CV of rec. catch	0.2	F	0.2	Weight on model fit
CV of comm. catch	0.1	F	0.1	Weight on model fit
CV of recruitment	0.5	F	0.5	Weight on model fit
CV of Index catch	0.2	F	0.2	Weight on model fit
Selectivity age-0 12"	0.1	F	0.1	Age-specific component of directed fishing mortality used in projection
Selectivity age-1 12"	1	F	1	Age-specific component of directed fishing mortality used in projection
Selectivity age $\geq 2$ 12"	1	F	1	Age-specific component of directed fishing mortality used in projection
Selectivity age-0 13"	0.05	F	0.05	Age-specific component of directed fishing mortality used in projection
Selectivity age-1 13"	0.8	F	0.8	Age-specific component of directed fishing mortality used in projection
Selectivity age $\geq 2$ 13"	1	F	1	Age-specific component of directed fishing mortality used in projection
Selectivity age-0 14"	0.03	*E/F	0.03	Age-specific component of directed fishing mortality used in projection
Selectivity age-1 14"	0.6	*E/F	0.54	Age-specific component of directed fishing mortality used in projection
Selectivity age $\geq 2$ 14"	1	*E/F	1	Age-specific component of directed fishing mortality used in projection
Unexploited stock size	455,000	E	492,000	Virgin stock size used to estimate benchmark SPR
Index selectivity (all ages)	1	E	0.2 (age-0) 0.8 (age-1) 1 (age-2+)	Age-specific catchability of gillnet survey

\*Selectivity values for 14" limit were used for initial optimization and were estimated. These values were then fixed for the projection.

al. 2006). The ASAP2 model was used (1) to estimate stock status (1993–2005) of *C. nebulosus* including estimates of SSB and age-specific fishing mortality rate ( $F_a$ ), (2) to estimate uncertainty for current stock status, and (3) to conduct projections of relative SSB and female fishery yield for a range of management scenarios (See Model projections section). The model input data were for females only because of our emphasis on the influence of management on reproductive capacity and population stability. The influence of management on relative fishery yield is presented as a tool for discussing the tradeoffs between population stability and harvest but is not a measure of total fishery yield as about 14% of the total harvest is estimated to be male (Figure 2A).

Reference benchmarks for the fishery were selected based on common benchmarks used for stock assessments of *C. nebulosus* in other states (GSMFC 2001). No benchmarks have been established for *C. nebulosus* in Mississippi, however several other states have chosen reference points based on SPR (Table 1). For this assessment we report MSY, Fishing mortality rate at MSY ( $F_{msy}$ ), SSB<sub>msy</sub>, and Fishing mortality rate at an SPR of 30% ( $F_{30}$ ). Fishery reference points are addressed in more detail in the Discussion.

Uncertainty estimates for model output including fishery benchmarks were based on a Markov Chain Monte Carlo

(MCMC) simulation involving 200 model runs selected from 200,000 overall runs with an initial burn in of 1,000 runs. Each run is a repeat of the base model with randomly selected values for each input parameter from the appropriate distribution with the best fit parameter value as the mean. The MCMC approach is a well-established method for estimating uncertainty in model estimates based on variability in model parameters (Haddon 2001). All parameters were assigned a lognormal error structure with the exception of catch at age data which were assigned a multinomial error structure. In addition a retrospective analysis was conducted that involved a series of model simulations with the final year reduced by 1 to identify any retrospective patterns in the data time series.

#### Model projections

The baseline results of the SCAA model were projected forward for a period of 12 yr (2003–2015) based on a range of both management actions and biological conditions. This projection period was chosen to allow for an initial transition period (~5 yr) to a stable outcome. Projections were conducted at three length limit restrictions 12", 13" and 14" and 4 projected fishing mortality rates ( $F_{current}$ , 125% of  $F_{current}$ , 150% of  $F_{current}$ , and  $F_{30}$ ). Length limits were simulated with shifts in the age-specific selectivity of the fishery in the model (Table 2). Selectivity changes were based on the

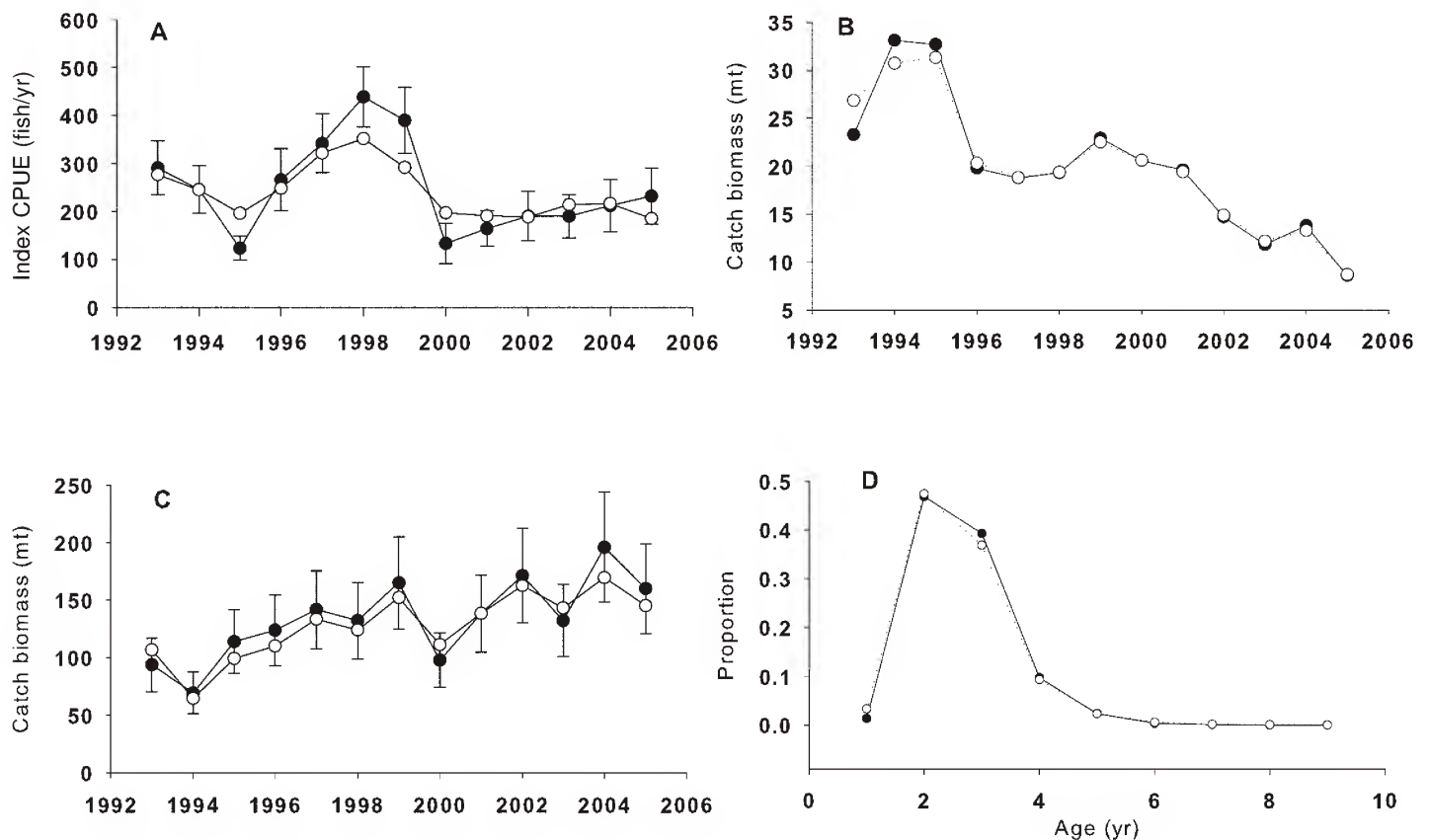
probability of a legal sized fish being in a particular age class, which was estimated using a cumulative ALK (1993–2005; CFRD unpublished data). These age-specific probabilities were also adjusted to account for delayed release mortality of sub-legal fish based on reported numbers of fish released alive (NMFS Fisheries Statistics Section unpublished data) and an estimated 72 h mortality rate of 10% based on an observational study ( $n = 478$  fish; R. Hendon, unpublished data). All other components of the base model run remained consistent with the optimized results given in Table 2. In addition, these projections were repeated with one of 2 recruitment patterns. Either annual recruitment of age-0 fish was allowed to shift according to the model-estimated stock recruitment curve or age-0 recruitment was held constant at an average value for the last 5 yr of the dataset (2000–2005). The constant recruitment option assumes that recruitment may have reached a biological maximum (e.g., habitat limitation). The output from these projections is a time series for SSB and fishery yield over the proceeding 5 yr based on management and biological conditions. Output from model projections was relative change in SSB and female yield expressed as the proportion of either SSB or yield in 2006 under current conditions for length limits and fishing

mortality. Differences between the model projections were based either on differences in linear slope analyzed with an ANCOVA or differences in terminal year value with an ANOVA.

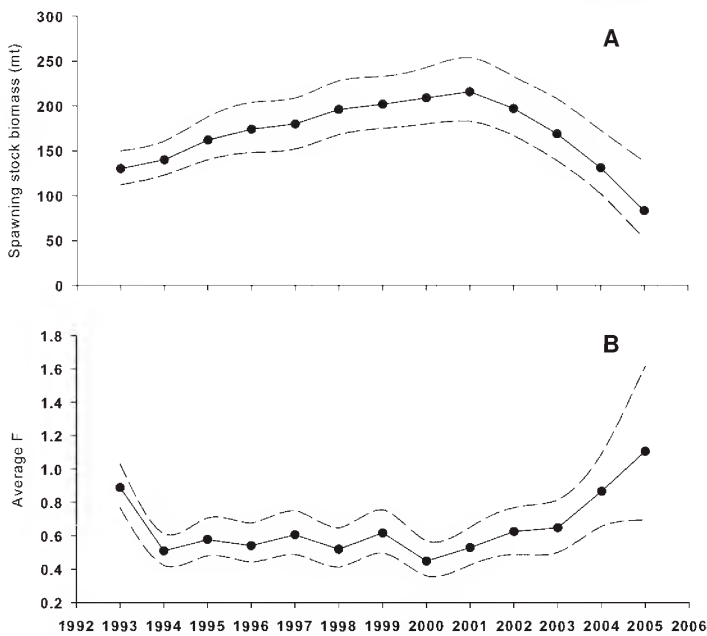
## RESULTS

The SCAA model provided a good fit to the overall objective function with most of the error contained in the fit to fishery age composition (71%). This was expected as the age composition of the catch was dominated by age-1 and age-2 fish leaving little latitude for the model fit. Most of the lack of fit occurred as an overestimation of age-1 fish and underestimation of age-2 fish in the catch, but the total deviance was small (Figure 3). The stock recruitment function provided a meaningful constraint on the abundance of age-0 fish each year with a final steepness value of 0.8.

The MCMC and retrospective analyses indicated a low level of variability about the predictions of average  $F$  (across age classes) and SSB with a generally increasing pattern in uncertainty towards the final year in the assessment (Figure 4). In addition, the retrospective analysis suggested retrospective pattern in the model fit was present with strongest influence in the final 2 yr of the assessment with CV in-



**Figure 3.** SCAA model fit. A. Index CPUE. B. Total commercial catch biomass. C. Total recreation catch biomass. D. Age composition of the recreational catch pooled across years. Closed symbol indicates observed data and open symbol indicates prediction of the age-structured model. Error bars are  $\pm 1$  se.



**Figure 4.** Time series of model simulations based on a Monte Carlo analysis. A. Median spawning stock biomass (SSB). B. Average fishing mortality rate (F). Solid line—Monte Carlo analysis, dashed error lines—5th and 95th percentiles.

creasing to  $> 1$ , so projections were initiated in 2003 and run for an additional 2 yr (i.e., final projection year 2015) to minimize the effects of retrospective pattern on the projections. Overall variability in model estimates (model CV 16%, 1993–2005) was used to analyze projection results.

Spawning stock biomass in 2003 was estimated in the model to be 169 mt (95% CL 75–426 mt) and the probability that  $SSB_{2003}$  exceeded  $SSB_{msy}$  was estimated to be 71% (Figure 5A). The model estimated an increasing trend in SSB between 1993 and 2001 and then a decreasing trend until 2003 (Figure 4A). The net change in SSB between 1993 and 2003 (39 mt) was estimated to be greater than the uncertainty of model output (95% CI  $\pm 23$  mt), suggesting a significant increase over this period.

Fishing mortality rate in 2003 was estimated to be 0.65 (95% CL 0.50–0.82). The probability that current  $F$  exceeds  $F_{msy}$  is about 17% (Figure 5B). The trend in average fishing mortality was positive over the entire time series (Figure 4B), however the trend is flat from 1994 to 2000 after which  $F$  began to rise more rapidly suggesting most of the increase in fishing mortality has occurred in recent years.

Forward projections of the model indicated that changes in the trend in relative female yield for the recreational fishery changed as a function of length limits, but the magnitude and direction of change is dependent on the level of fishing mortality and the projected recruitment rate (Figure 6). Using the model stock recruitment function and  $F$  at or above  $F_{current}$ , relative female yield was at or above 1 in 2006 at all size limits (Figure 6A, C, E). Relative female yield increased initially at all size limits for  $F_{current}$  and 125% of  $F_{current}$ , but then began to decrease after 2008 with

the most rapid decrease for the 12" size limit. The slope of relative yield at 12" was significantly different (ANCOVA;  $p < 0.008$ ) than either 13 or 14" at  $F_{current}$  and at 125% of  $F_{current}$ . The slopes were all negative at 150% of  $F_{current}$ , but were not significantly different ( $p = 0.074$ ). At  $F_{30\%}$  relative female yield increased monotonically to over 200% of the yield in 2006 with no significant difference in slope between length limits (ANCOVA;  $p = 0.3$ ; Figure 6G).

The influence of length limits and fishing mortality rate on relative yield were reduced if recruitment of age-0 fish was capped at the 5 yr average (Figure 6B, D, F, H). Relative yield declined initially for all  $F$  at or above  $F_{current}$ , but the slope increased to near zero by 2010. For  $F_{30\%}$  the trend was initially positive and then flat after 2008 for the rest of the projection period (Figure 6H). However, no significant differences in slope were detected ( $p > 0.1$ ) among length limits at any value of  $F$ . The stable value for relative yield after 2010 was not significantly different among levels of  $F$  (ANOVA;  $p > 0.1$ ) or among length limits (ANOVA;  $p > 0.1$ ). This recruitment driven stable point for the projection was 60–70% of the estimated female yield in 2005.

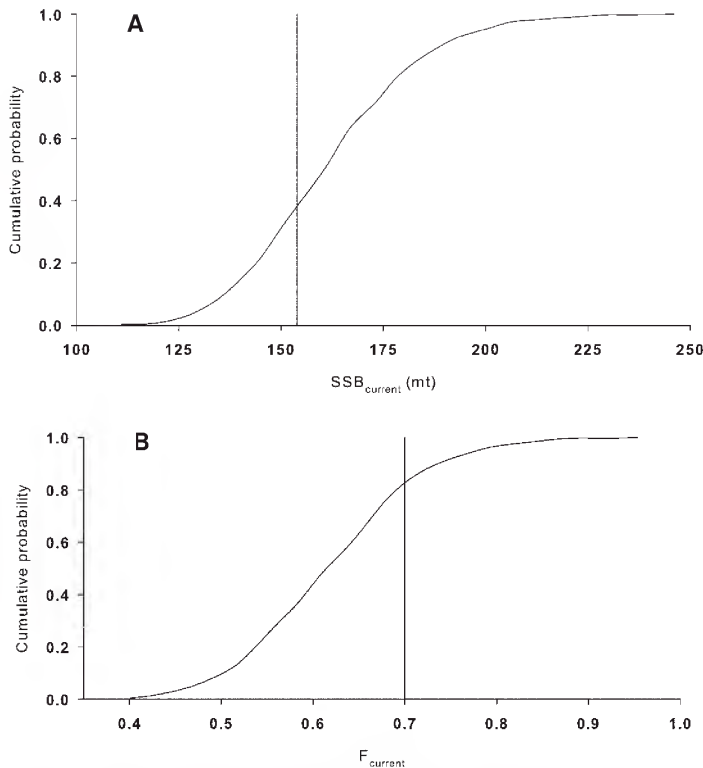
Spawning stock biomass was also projected to be influenced by length limit, recruitment pattern, and fishing mortality rate (Figure 7). If a stock recruitment function was used in the projection with  $F = F_{current}$ , SSB was predicted to increase by 66% by 2015 with a length limit of 14", but decline by 23% and 53% at 13" and 12" respectively (Figure 7A). If  $F$  was set at either 125% or 150% of  $F_{current}$ , then the trend in SSB had a negative slope for all length limits with SSB declining by 60–80% at 125% of  $F_{current}$  and 80–95% at 150% (Figure 7C, E). The slope for 12" was significantly lower at 125% of  $F_{current}$  (ANCOVA,  $p = 0.004$ ) than the slope at either 13" or 14". No significant difference in slope was detected at 150% of  $F_{current}$  ( $p = 0.64$ ). For  $F_{30\%}$  the projected trend in SSB had a strongly positive slope for all three length limits with the slope at 12" significantly lower ( $p < 0.001$ ) than at either 13" or 14" (Figure 7G).

Model projections of SSB changed somewhat when recruitment of age-0 fish was capped at the 5 yr average (Figure 7B, D, F, H). Projected SSB between 2003 and 2015 declined initially for all length limits and all  $F$  at or above  $F_{current}$ . The

**TABLE 3.** Model generated reference benchmarks for the *C. nebulosus* recreational fishery in Mississippi. Values in parentheses are 95% confidence limits.

Benchmark	Estimated value
$F_{current}$	0.65 (0.50–0.82)
$F_{msy}$	0.7 (0.63–0.77)
MSY	24.9 mt
$SSB_{msy}$	120 mt (15–453)
$F_{30\%}$	0.37





**Figure 5.** Cumulative density function the model run based on Monte Carlo analysis. A. Spawning stock biomass (SSB). B. average  $F_{current}$  for the terminal year. Vertical lines indicate model estimates of  $SSB_{msy}$  and  $F_{msy}$  respectively.

trend was flat for all length limits at  $F_{30\%}$  (Figure 7H). All projections with a fixed recruitment rate stabilized by 2010 and the final year SSB differed by level of  $F$ , but only the ending value at  $F_{30\%}$  (21% increase from 2003) differed significantly from the other three values of  $F$  examined (ANOVA,  $p < 0.03$ ).

## DISCUSSION

Projections made with an SCAA model are sensitive to uncertainty in future conditions such as recruitment and fishing effort. In some cases, patterns in future conditions can be well estimated and used to make specific predictions of future stock status (Mohr et al. 2007, Hoff and Frost 2008, Reich and DeAlteris 2009). In the case of *C. nebulosus* in Mississippi, too much uncertainty exists regarding future recruitment and angler behavior to make predictions. Yet, we can project the state of the stock in the future relative to current conditions and in so doing gain some useful insight on the sensitivity of the population to specific actions. There is both process uncertainty and observation uncertainty present in such projections that are difficult to separate and quantify. However, the use of an MCMC approach to estimate overall uncertainty should allow for a combined estimate, which allows for an estimate of the risk of exceeding benchmarks associated with specific management actions, as well as trends in relative stock condition through time.

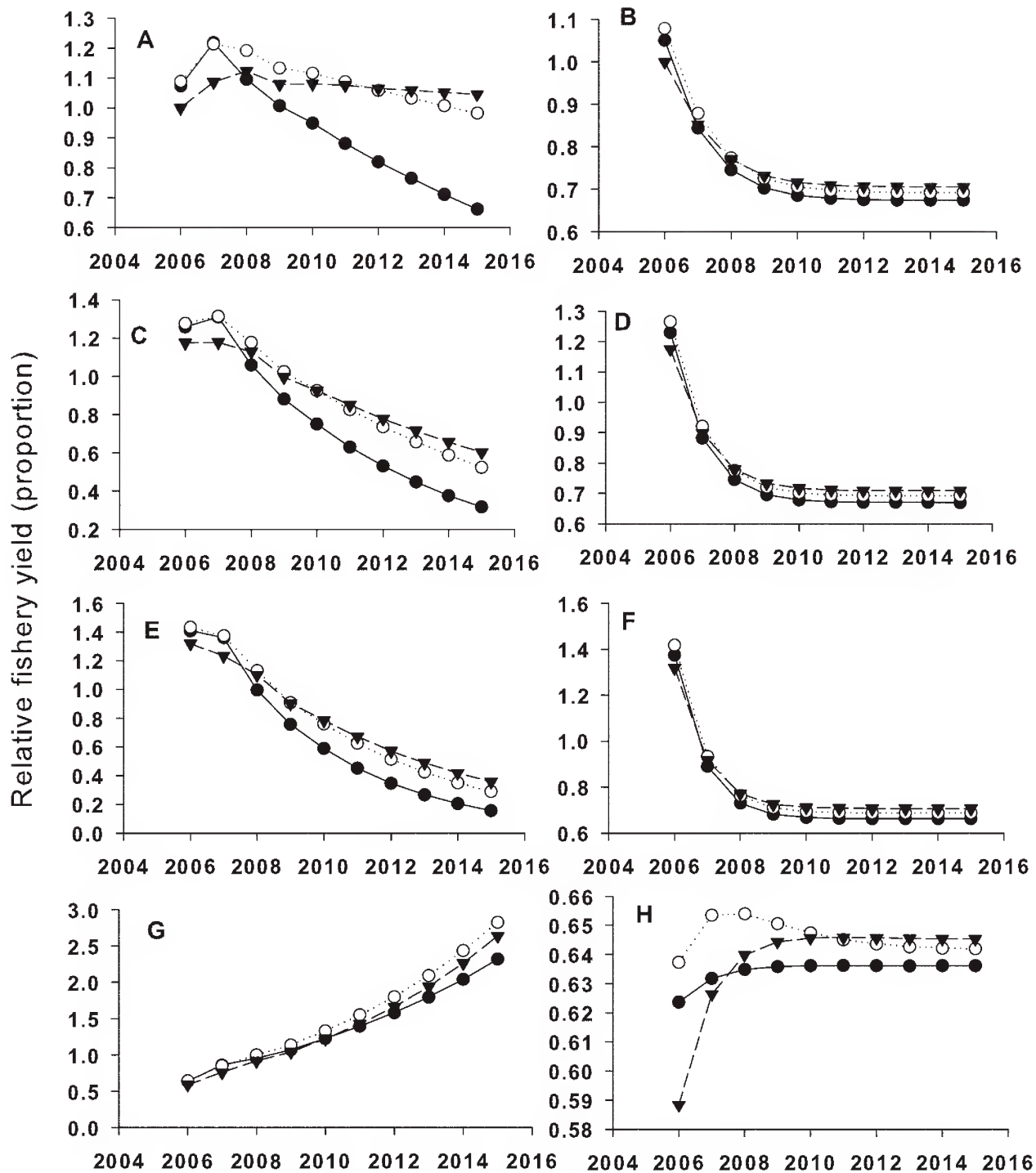
The results of the model analysis indicate that the influ-

ence of changes in the minimum legal length limit for *C. nebulosus* is dependent on both future recruitment and future changes in angler effort. Yet, certain consistencies did emerge across the range of length limits tested in the model. The largest length limit of 14" produced the highest relative yield in the terminal year and the highest SSB in all but the most conservative level of fishing mortality rate. In contrast, the smallest length limit (12") produced the lowest terminal year relative yield and the lowest projected SSB in all simulations. There was variance in the similarity of projected outcomes for a length limit of 13" and it seems that 13" and 14" differ most as management actions under current conditions and are more similar if fishing mortality is either raised or lowered significantly. Fishing at  $F_{30\%}$  always produced the highest yields and the largest increase in SSB across all minimum length limits. In the case of  $F_{30\%}$ , relative yield may not comprehensively emulate objectives for a recreational fishery, as this increase is driven by the increase in abundance of larger, older fish. The model indicated that stock abundance would increase as well, but not as much as yield.

When recruitment was held constant at the 5 yr average, the projection results always stabilized after about 5 yr and remained constant thereafter. The exact level of stability was dependent on fishing mortality rate, but not on the minimum length limit, which suggests that if current recruitment levels are limiting then a lot of fishery yield is lost as pre-recruit mortality even at lower levels of  $F$ . This finding supports the idea that recruitment limitation (e.g., via habitat loss) may be as important as management actions to fishery yield.

Recruitment of *C. nebulosus* in coastal Mississippi has not been comprehensively examined, but research suggests coastal aquatic vegetation is an important limiting component. *Cynoscion nebulosus* has been shown to be highly dependent on rooted macrophytes for nursery habitat (Rozas and Minello 1998, GSMFC 2001), and a study of nursery source habitat in Mississippi Sound indicated that a higher proportion of adults had a chemical signature consistent with a nursery area having a higher than average density of sea grasses (Comyns et al. 2008). Juveniles may also be using emergent macrophytes such as salt marsh as habitat (Chester and Thayer 1990), but studies have found a strong preference for both emergent and submerged rooted macrophytes (GSMFC 2001). Both submerged sea grass and emergent marsh have been in general decline in coastal Mississippi (Moncreiff et al. 1998) and this suggests that nursery habitat may be in decline, which will contribute to limiting future recruitment to the fishable stock.

If nursery habitat might be limiting to recruitment in the future, it becomes more important to establish an SPR benchmark that is adequate to allow for reductions in juvenile survivorship. Only one scenario was tested that involved a theoretical benchmark SPR ( $F_{30\%}$ ) and the result was much higher SSB with a stock-recruitment relationship, but no



**Figure 6.** Model-based projections of relative female yield for the *Cynoscion nebulosus* recreational fishery. Relative fishery yield is expressed as proportion of estimated yield in 2006 under current conditions for  $F$  and minimum length limits. Panels are for 4 levels of fishing mortality (A, B -  $F_{current}$ ; C, D -  $125\% F_{current}$ ; E, F -  $150\% F_{current}$ ; and G, H -  $F_{30\%}$ ) and either model predicted (left) or constant (right) recruitment. Each panel contains a projection for 3 theoretical length limits: 12" (●), 13" (○), or 14" (▲). See text for details.

real difference if recruitment was capped. This outcome demonstrates that management actions to mediate loss of essential habitat may have limited value once the habitat is lost.

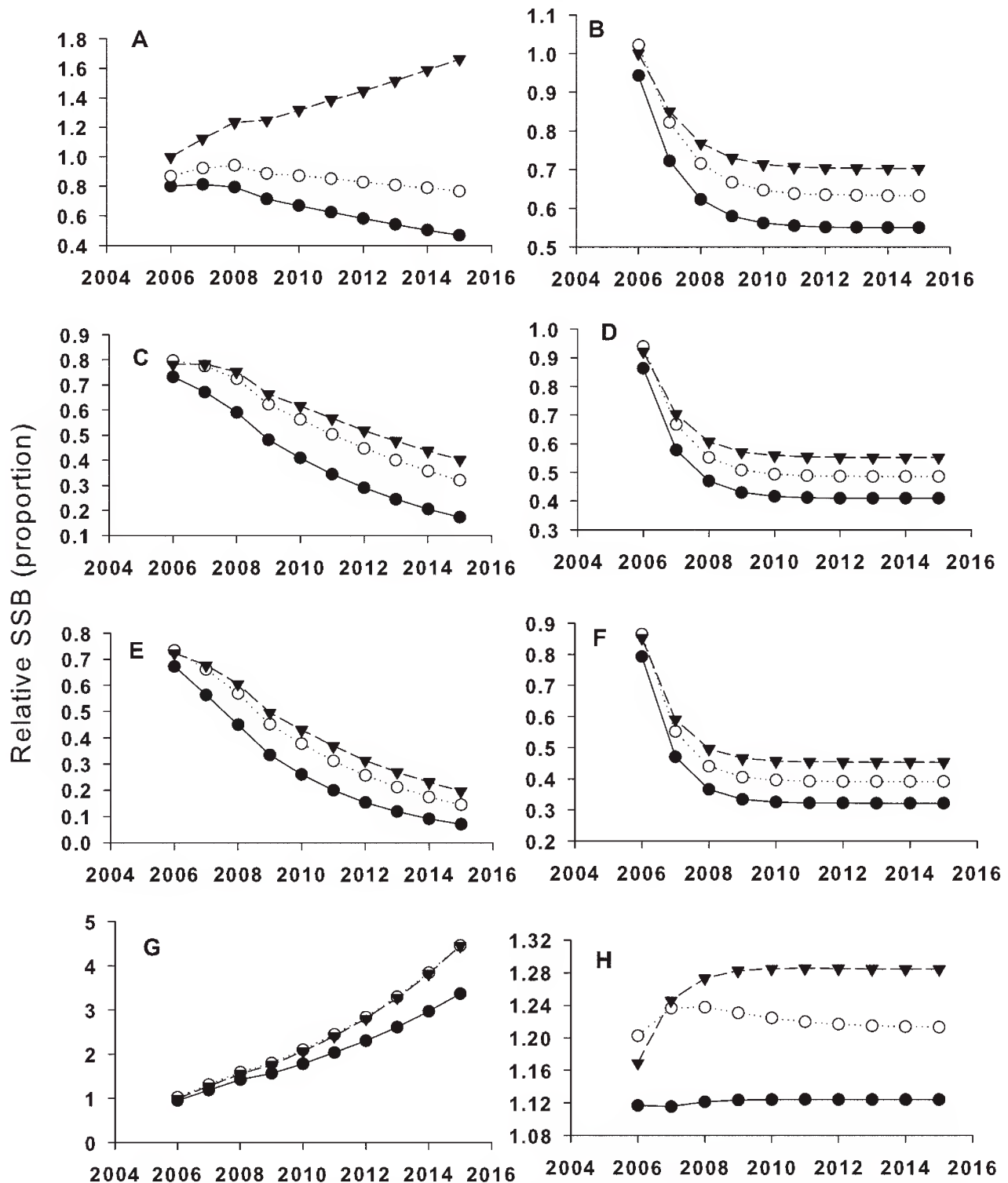
While Mississippi does not have a target SPR, data suggest the current SPR of the Mississippi stock is below the reported target values for other GOM states (Table 1). The

transitional SPR has been independently estimated to be between 6 and 13% from 1993 to 2005 (R. Hendon, unpublished data). The applicability of these benchmark values for the Mississippi stock has not been evaluated and our use of  $F_{30\%}$  should not be interpreted as an endorsement of this value for management. Yet, our model projections suggest

that allowing stock SPR to fall further is likely to result in a declining SSB and relative yield, while increasing SPR ultimately will both increase yield and SSB, despite the decline in harvest needed to accomplish this objective. Changes in the minimum length limit should influence stock SPR, as

indicated by changes in projected SSB in the model, but other factors affecting fishing mortality are also important.

Changes in fishing mortality not associated with management regulations are most strongly affected by changes in angler effort. Angler effort in the future is highly uncertain as



**Figure 7.** Model-based projections of relative spawning stock biomass (SSB) for *Cynoscion nebulosus*. Relative biomass is expressed as the proportion of SSB estimated in 2006 under current conditions for  $F$  and minimum length limits. Panels are for four levels of fishing mortality (A, B -  $F_{current}$ ; C, D -  $125\% F_{current}$ ; E, F -  $150\% F_{current}$ ; and G, H -  $F_{30\%}$ ) and either model predicted (left) or constant (right) recruitment. Each panel contains a projection for three theoretical length limits: 12" (●), 13" (○), or 14" (▲). See text for details.



recreational fishing has been shown to respond to a variety of influences including costs of fishing, individual objectives of fishing (e.g., food vs. trophy fishing), and angler access (GSMFC 2001). In the case of *C. nebulosus* in Mississippi, creel data indicate that angler effort has increased from around 800,000 trips/yr in 1993 to over 1,000,000 trips/yr between 2000 and 2004 (MS-DMR unpublished data). Model results suggest that while fishing mortality has been consistently close to  $F_{msy}$  since 1993, recreational catches have been slowly increasing over this time period. Commercial catches have been falling but this is thought to be a result of declining effort. This suggests that both population abundance and angler effort have increased since 1993. The model estimated an increasing trend in  $F$  and a decreasing trend in SSB since 2000, which further suggests that population abundance may have reached a peak while angler effort continues to rise. If this is true, any increase in fishing mortality due to changes in the length limit would only increase this trend.

Creel data indicate that a reduction in the legal length limit for *C. nebulosus* may also result in an increase in angler effort in the future. Fish size distribution appears to shift upwards away from shore due to the higher abundance of mature females associated with the barrier islands (GSMFC 2001), so there is a presumed negative relationship between minimum length limits and angler access since shore-bound or small boat anglers have more access to smaller fish. The true response is highly uncertain. In fact there is a high reported catch and release for near shore sub-legal fish when the length limit is 14" (MS-DMR, unpublished data), and a reduction in the size limit may result in a transfer of release mortality into harvest. However, data also suggest release mortality, even after 72 h, is less than 10% (R. Hendon, unpublished data), and while illegal harvest may increase this number, it remains likely that a reduction in the length limit is likely to increase the target value of *C. nebulosus* and result in more angler effort.

The model projections combining lower length limits (12–13") with increased fishing mortality are more likely to be consistent with angler behavior under these assumptions. The current average  $F$  for female *C. nebulosus* in Mississippi is very close to  $F_{msy}$ . Our analysis suggests that after accounting for uncertainty, population stability is more likely if  $F$  remains stable or is reduced. In particular, the recent downward trend in SSB suggests that any further increase in harvest will negatively affect SPR.

Independent of angler response, model results suggest a 14" size limit is most consistent with maintaining or increasing SPR. Estimates of SPR for *C. nebulosus* in Mississippi appear very sensitive to fishing mortality for age-1 fish. *Cynoscion nebulosus* are 80% mature by age-2 but only 45% mature at age-1 (Brown-Peterson and Warren 2001) and data suggest they have a mean size of 12" at age-1 and a mean size of 14.6" at age-2 (CFRD unpublished data).

Based on model input data and accounting for differences in length-specific fecundity (Brown-Peterson and Warren 2001), annual egg production is 41% from age-1 and 44% from age-2 fish, so spawning potential is highly dependent on newly-mature age-1 and age-2 fish and should be very sensitive to an increase in mortality for these fish. The best strategy for population stability, based on model results, is to protect age-1 fish until they spawn at least once. Model projections indicate this strategy might be possible at either a 13 or a 14" length limit, but after accounting for future uncertainty is most likely with a 14" length limit. The positive trend in SSB predicted by the model between 1993 and 2000 also suggests that the 14" size limit combined with lower angler effort resulted in a stable population over this period.

Statistical catch at age models are valuable tools for both estimating stock status and projecting the effects of future changes in condition. One key strength of the approach is the ability to account for uncertainty in the model estimates. Uncertainty can have many sources but the most common are uncertainty due to model structure (i.e., process) and uncertainty due to variability in the data (i.e., observation uncertainty). In particular the model is sensitive to observation uncertainty present in estimates of catch at age taken from MRFSS surveys. The MRFSS program has been criticized for observer bias and inconsistent levels of coverage through time (NRC 2006). This has resulted in a high coefficient of variation between years for these data that must be carried through to model output. In this case, the importance of these data to overall model fit was down-weighted to partially account for bias in the MRFSS data and its influence on uncertainty estimates is thought to be small.

*Cynoscion nebulosus* should be managed on a state by state basis based on the results of tagging (e.g., Hendon et al. 2002) and genetic (Gold et al. 1999) studies. Several states along the Gulf Coast have established SPR-based benchmarks for assessing stock status but over a fairly broad range of relative SSB (Table 1). Our results suggest that in Mississippi, the most robust strategy is to protect SSB at age-1 in order to maintain a high level of recruitment. *Cynoscion nebulosus* is the dominant sportfish in coastal waters (GSMFC 2001) with a higher directed effort on this species in comparison to other neighboring states with a more diverse inshore fishery. While it is difficult to make a definitive statement regarding why the Mississippi fishery may require more conservative benchmarks for population stability it is likely related to this high directed effort and the decline in coastal vegetation over time. In general it will be important to set meaningful benchmarks for population stability that reflect local conditions, and these actions can be appropriately evaluated using quantitative tools such as SCAA models prior to implementation, which should greatly improve the manager's ability to maintain a stable and productive fishery for the future.

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Effects of Hurricane Katrina on an Incipient Population of Giant Salvinia *Salvinia molesta* in the Lower Pascagoula River, Mississippi

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**SHORT COMMUNICATION****EFFECTS OF HURRICANE KATRINA ON AN INCIPIENT POPULATION OF GIANT SALVINIA *SALVINIA MOLESTA* IN THE LOWER PASCAGOULA RIVER, MISSISSIPPI**Pam L. Fuller<sup>1</sup>\*, Mike G. Pursley<sup>2</sup>, Dale Diaz<sup>2</sup>, and Wesley Devers<sup>2</sup><sup>1</sup>U.S. Geological Survey, 7920 NW 71<sup>st</sup> Street, Gainesville, FL 32653 USA, <sup>2</sup>Mississippi Department of Marine Resources, 1141 Bayview Avenue, Biloxi, MS 39530 USA \*Corresponding author, email: pfuller@usgs.gov**INTRODUCTION**

Giant salvinia (*Salvinia molesta*) is among the worst invasive aquatic weeds in the world (Holm et al. 1977) and has invaded aquatic habitats in numerous countries (Julien et al. 2002). Under ideal conditions giant salvinia can double its biomass within 2 (Cary and Weerts 1983) to 4 d (Gaudet 1973, Mitchell and Tur 1975, Sale et al. 1985), clogging waterways with dense mats of vegetation. A single plant is capable of starting a population that may cover 103.6 km<sup>2</sup> (40 mi<sup>2</sup>) in 3 mo (Creagh 1991/1992 in Jacono and Pitman 2001). Giant salvinia can out-compete native vegetation and if control measures are not implemented, will completely cover the water surface and form mats up to 1 m thick (Creagh 1991/1992 in Oliver 1993). These mats deplete dissolved oxygen, make waterways uninhabitable by most fish species, impede boat traffic, reduce habitat for waterfowl, limit access for fishing and swimming and can interfere with water use for electrical generation, irrigation and municipal water supplies (Julien et al. 2002).

Giant salvinia has been listed as a Federal Noxious Weed since 1984 (McFarland et al. 2004), and as such, it is illegal to import into, or transport this plant within the United States. Giant salvinia also appears on many state noxious weed lists, including Mississippi's (U.S. Department of Agriculture 2009). However, if giant salvinia is not declared by a state as a noxious weed, it can still be cultivated and sold within that state. Despite regulations, this species continues to be moved through the water garden trade as an ornamental plant for backyard ponds. Escapes or releases from such areas may have resulted in its establishment in numerous southern states such as Florida, Louisiana, and Texas and in major waterways like the Colorado River (U.S. Geological Survey 2009).

A population of giant salvinia was discovered in June 2005 in the lower west Pascagoula River distributary and a major tributary, Bluff Creek, in Jackson County, Mississippi. At the first report of infestation, the Mississippi Department of Marine Resources (MDMR) conducted an initial survey of the watershed and determined that giant salvinia was restricted to areas on the western side of the river both north and south of Interstate 10 and was densest in backwater sloughs

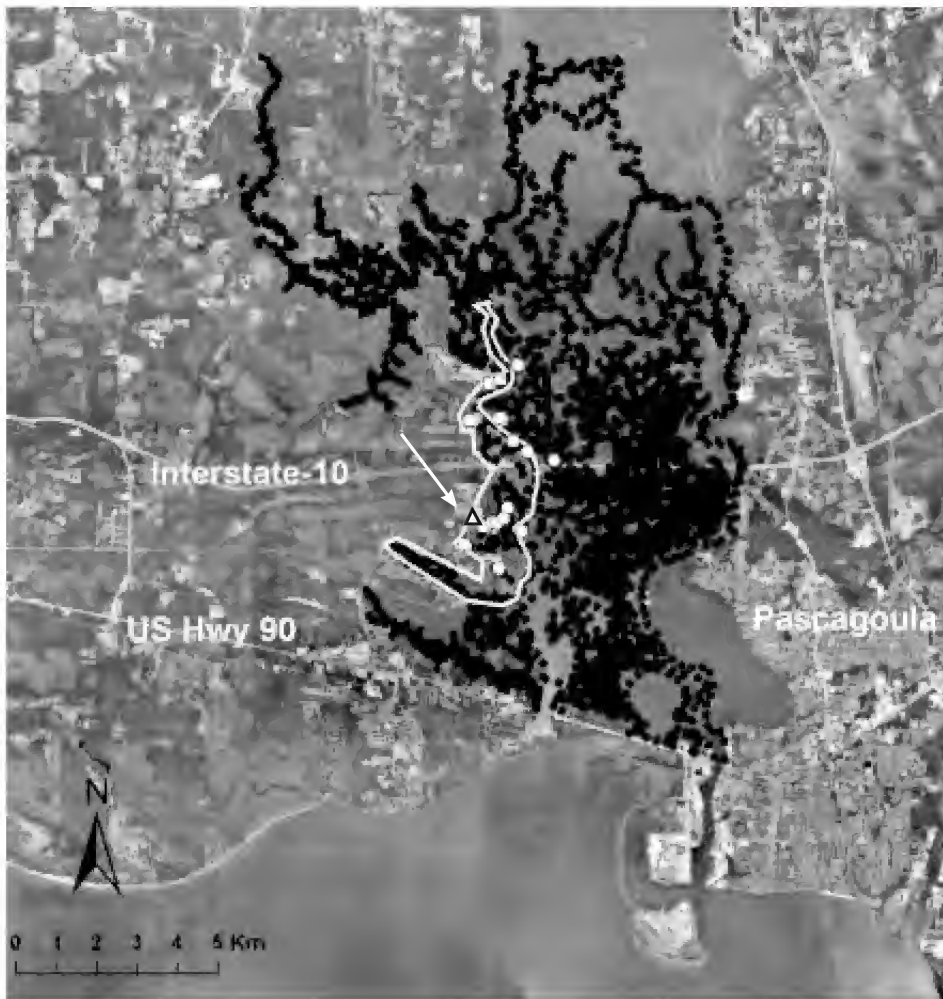
(Figure 1). Biologists from MDMR also concluded that the infestation had become too extensive (about 789 ha) to eradicate with herbicides or mechanical control methods, so Australian salvinia weevils (*Cyrtobagous salviniae*) were chosen as a bio-control agent. The weevils were seeded in 3 locations on 18 August 2005 in an effort to establish a population that would ultimately hinder the spread. An outreach campaign, in the form of signs at boat ramps and other high-visibility areas, was also initiated to increase public awareness of giant salvinia and on measures to prevent its spread. Interviews of local residents by MDMR indicate that the source of the infestation was likely a direct release of the plant during a clean-out of a water garden pond. The densest area of infestation was in a canal that drains a residential area just south of I-10.

Hurricane Katrina struck the Mississippi coast 29 August 2005 causing a storm surge in the study area ranging from 4.6–5.2 m (FEMA 2005). At the time, there was concern and speculation over the fate of the giant salvinia. Several hypotheses were considered to have merit: 1) The storm surge may have beached much of the plant material on land, rendering the population small enough for control efforts; 2) the salinity of the surge may have killed at least the downstream portion of the infestation; 3) the plant may have been spread to new areas during the flooding; and 4) the growth and spread of remaining giant salvinia may be augmented by increased nutrient levels resulting from the flooding.

The objectives of this study were to: 1) survey the lower Pascagoula River Basin and determine the post-storm distribution and abundance of giant salvinia; 2) control any remaining giant salvinia through physical and/or chemical means; 3) determine the fate of the bio-control agents; and 4) determine if re-introduction of salvinia weevils is needed and if so, to decide where best to release them.

**MATERIALS AND METHODS**

The study area consisted of about 483 km of navigable waterway of the lower Pascagoula River system from near the river mouth at Highway 90 to about 11.26 km north of Interstate 10 (Figure 1). The extent of the survey area was chosen



**Figure 1.** Area of the lower Pascagoula River, Jackson County, Mississippi surveyed for giant salvinia after Hurricane Katrina. The area encompassed by the white line is the pre-storm infestation area. Black dots are survey points with no giant salvinia; white dots are areas where giant salvinia was found. White triangle (arrow) is Martin Bluff, where a population was found in June 2008.

based on pre-Hurricane Katrina giant salvinia presence and was expanded well beyond known pre-storm distribution to determine if the invasive plant had infiltrated other waterways.

Because all records were destroyed when Hurricane Katrina flooded the MDMR offices, pre-storm giant salvinia distribution was approximated and was mapped based on the recollection of MDMR staff. Mapping surveys documented the presence or absence of giant salvinia and other aquatic invasive plants post Hurricane Katrina at about 3,300 points over 37 field days between 1 May and 9 August 2006. Monthly follow-up surveys have been conducted from September 2006 to the present to look for new infestations of giant salvinia. Bi-weekly surveys have been conducted to monitor giant salvinia growth and to spray and/or remove any remaining plants in previously identified areas.

Initial mapping surveys were conducted using a 3 person crew. All crew members also served as invasive plant spotters to maximize detection probability. The speed of the survey

boat was kept under 10 kph to facilitate observation of small fragments of giant salvinia. A data point was created every 300 m. At each point, a Magellan Mobile Mapper CE using ArcPad 6.0 was used to record the presence or absence of giant salvinia and the presence of any other aquatic invasive plants. Surface water temperature and salinity were acquired using a YSI model 556 multi-probe meter and manually entered into the Mobile Mapper as meta-data for each location. Digital photos were also taken of invasive plants when found. Survey crews also looked for the presence of salvinia weevils at each location by examining the plants for signs of weevil damage to the leaves. In areas with relatively small, isolated infestations, the plants were removed from the water using a small screened net and secured for later disposal on land. At the end of each survey day, the boat was removed from the water and visually checked for invasive plant matter on the outside and inside of the boat to prevent introduction of invasives into other waters.

Follow-up surveys were less regimented and were performed by slowly cruising the area in a boat looking for areas with the plant. These surveys were combined with control spraying operations. A mixture of 1.5% glyphosate and 0.5% diquat was applied on the

remnants left by the storm every 10–14 d through October 2006, after which time no giant salvinia could be found. Monthly surveys of the formerly infested areas occasionally yielded small patches of giant salvinia from April 2007 to June 2008 in the canals north and south of I-10. These areas were treated by mechanical removal and/or herbicide application as noted above.

## RESULTS

The initial survey effort revealed that over 99% of the giant salvinia present prior to the storm was killed either by storm surge salinity or by being deposited on land. However, giant salvinia was found at 19 sites in 7 areas adjacent to the west Pascagoula River (Figure 1), totaling about 2 ha. Surprisingly, the infestation had not spread substantially. Only a few sites were located outside of the original area of infestation, and those were only a few meters from the original infestation. It was also surprising to learn that the surge did



not push the infestation farther upriver. The highest salinity where giant salvinia was found was 1.44, although Biber (2008) reported this species living in salinities of 7 in the lower Pascagoula River.

Two new or previously unknown populations of the plant were located during follow-up surveys. One population of mature tertiary-stage growth was well-hidden in a patch of thick torpedo grass (*Panicum repens*) in a private pond connected to the river by a culvert; the other was in a stand of emergent aquatic vegetation in a puddle at the very end of a silted-in canal. These plants were treated and eliminated.

In June 2008, during a regular survey, a 46.45 m<sup>2</sup> patch of rapidly reproducing young giant salvinia was found just north of Martin Bluff (Jackson County) adjacent to a large marshy area (Figure 1). No giant salvinia had been seen there since Hurricane Katrina. A few plants had been removed just south of this area in April 2006 and none were seen during subsequent surveys.

Although it was thought that all the giant salvinia had been eliminated as of summer 2009, more patches have appeared, likely from hidden areas in the marsh that were not detected. No salvinia weevils were found during any of the surveys.

## DISCUSSION

An extensive river survey determined that the giant salvinia population had been greatly reduced, rather than expanded, as a result of Hurricane Katrina. The reduction was attributed to deposition on land and mortality caused by exposure to salinity (see Biber 2008) during the storm surge. Evidence was found during the survey which may explain one way giant salvinia survived the storm surge. As water rose during Hurricane Katrina, giant salvinia was trapped in the framing of boat houses, which became completely submerged during the storm surge (Figure 2). As the water receded some of the giant salvinia likely fell from the framing and re-infested the area.

After three years, there is still no evidence that any salvinia weevils survived Hurricane Katrina. With most known infestations eliminated, weevil re-introduction is not practical, or advisable. The salvinia weevils would not have enough plant material to be sustained, and the giant salvinia they arrived on could cause a new outbreak.

Mississippi Department of Marine Resources will continue conducting monthly boat and quarterly aerial surveys to look for new infestations and will survey the affected areas every 2 weeks. They will also continue public outreach efforts such as signs at boat ramps and brochures at fishing camps,



**Figure 2.** Giant salvinia draped on rafters of a boat house along the Pascagoula River in the study area nearly a year after Hurricane Katrina.



particularly in areas with close proximity to the infestations.

The timing of this study was fortuitous as the remaining 2 ha of infestation could have easily exceeded the original 769 ha had no action been taken. The state was only able to respond because of the funding obtained for this study. Without a quick response, the infestation would have gotten out of control and become too large to manage. The small area of infestation was key in being able to effectively manage this population of giant salvinia. From the discovery in June 2005 until October 2009, MDMR estimates expenditures of over \$256,000 on equipment, personnel, herbicides, and fuel and 2,110 person-hours to combat the invasion.

Eradication of giant salvinia in all but small enclosed bodies of water has been deemed to be very unlikely, and even then will likely take years (McFarland et al. 2004). Given the size of the lower Pascagoula River, the complexity of its channels and emergent vegetation, and the fact that another population of giant salvinia exists 235 km up-river in the Lower Leaf River (Robles et al. 2008), eradication seems unlikely in this area. However, because Hurricane Katrina reduced the population down to a manageable level, it appears that the state may be able to keep population levels low enough to control them in this area.

### ACKNOWLEDGEMENTS

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Notes on the Biology of an Adult Female *Chimaera cubana* Captured Off St. Croix, U.S. Virgin Islands

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## SHORT COMMUNICATION

NOTES ON THE BIOLOGY OF AN ADULT FEMALE *CHIMAERA CUBANA* CAPTURED OFF ST. CROIX, U.S. VIRGIN ISLANDS

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## INTRODUCTION

Within the western North Atlantic Ocean there are at least 4 genera and 5 species of chimaeroids occurring in deep waters generally associated with outer continental slopes or areas of high bathymetric relief (Didier 2002; Didier 2004). Two chimaeroids, *Chimaera cubana* and *Hydrolagus alberti*, are known to be indigenous to the Caribbean Sea in waters associated with the Greater and Lesser Antilles. While *H. alberti* occurs throughout the Gulf of Mexico and the Caribbean Sea, *C. cubana* is thought to be endemic to an area bounded by Cuba and Colombia (IUCN 2009). These two chimaeras are readily differentiated by the presence or absence of an anal fin and species-specific branching patterns of cranial lateral line canals (Didier 2004). Since the description of *C. cubana* by Howell-Rivero (1936), only 10 specimens have been reported in the primary literature with another 11 specimens located in museum collections (Bunkley-Williams and Williams 2004). The dearth of biological information on *C. cubana* led the International Union for the Conservation of Nature to recommend that "basic data be collected on all captures" (IUCN 2009).



**Figure 1.** Lateral view of the adult female *Chimaera cubana* collected south of St. Croix, U.S. Virgin Islands, on 25 March 2009. The right side of the fish is presented due to damage to the left pectoral and pelvic fins. Note that the preopercular and horizontal canals have separate branching points from the suborbital canal.

## MATERIALS AND METHODS

On 25 March 2009 an adult female *C. cubana* was captured on longline gear off St. Croix, U.S. Virgin Islands, at 17°38.25'N, 64°48.26'W between 2017–2144 h at a depth of 280 m. The bottom temperature, dissolved oxygen and salinity at the site were 18.3°C, 5.7 mg/l and 36.5, respectively. An incision was made through the abdominal musculature and the gastrointestinal and reproductive organs were excised. Fresh material was used for all examinations and photographs. The specimen was frozen after inspection, and later deposited in the museum at the University of Southern Mississippi, Gulf Coast Research Laboratory (accession number GCRL 36376). Anatomical terms used in descriptions follow Dean (1906), Wourms (1977) and Jones et al. (2005).

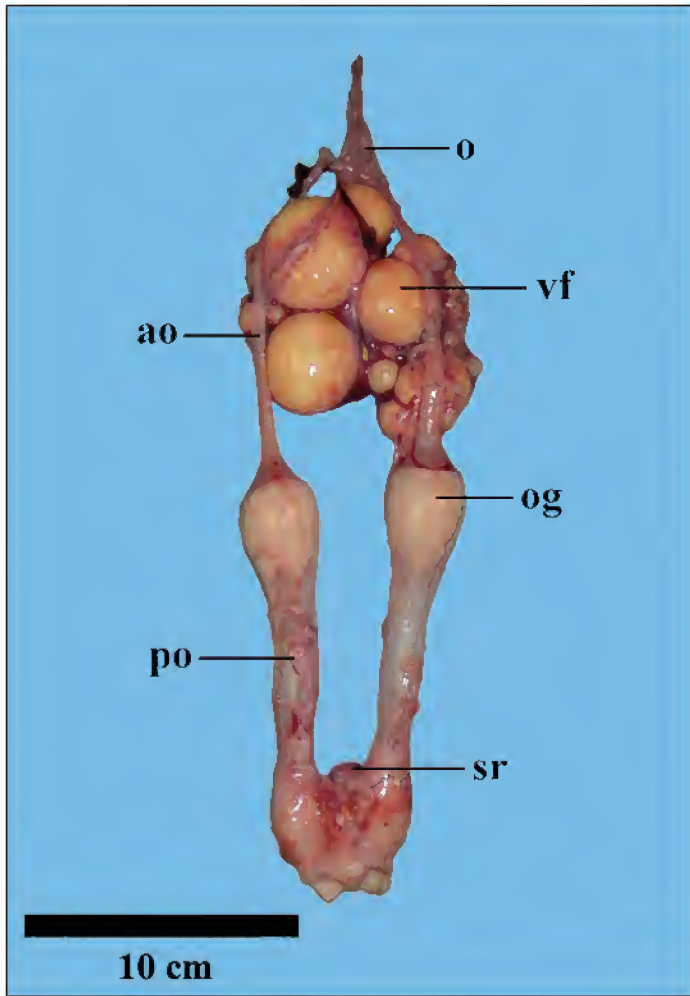
## RESULTS AND DISCUSSION

The specimen's anal fin, caudal fin and tail filament were missing (Figure 1), and thus a total length measurement was not taken. The distances from the snout to the pectoral fin origin and snout to the pelvic fin origin were 103 mm and 338 mm, respectively.

The digestive tract contained numerous *Clypeaster subdepressus* tests and ambulatory spines, suggesting these echinoderms could represent a significant prey item of *C. cubana*. Eight gyrocotylidean cestodes were distributed throughout the spiral intestine. Bunkley-Williams and Williams (2004) reported the presence of 2 specimens of a gyrocotylidean cestode in the spiral intestine of a *C. cubana* caught off La Parguera, Puerto Rico, and identified the specimens as *Gyrocotyle rugosa* or *G. urna*. We obtained the specimens reported by Bunkley-Williams and Williams (2004) from the United States National Parasite Collection (USNPC No. 92730) and found them to be conspecific with the specimens we collected. Based on diagnostic characters used to differentiate among the species within the genus (i.e., shape of the lateral body margin), we identified all of the specimens as *G. urna*. A forthcoming study will examine 28S rDNA fragments from the Caribbean, Norwegian and Australian specimens of *G. urna* to thoroughly assess the identity of Caribbean *Gyrocotyle* fauna.

The reproductive tract was typical of a female chimaeroid

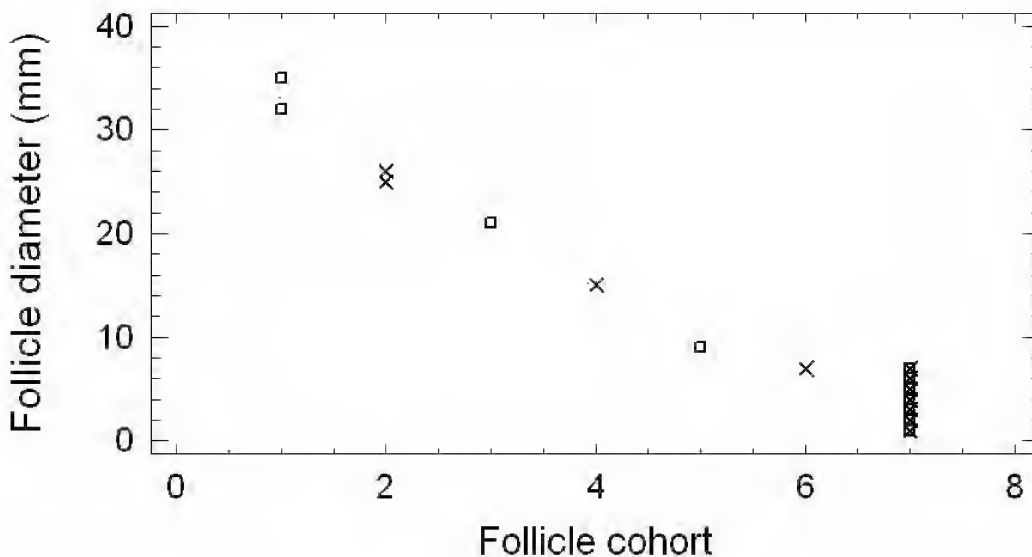




**Figure 2.** Reproductive tract of the adult female *Chimaera cubana* collected south of St. Croix, U.S. Virgin Islands on 25 March 2009. Note vitellogenic follicles in varying stages of development. ao = anterior oviduct, o = ostium, og = oviducal gland, po = posterior oviduct, sr = seminal receptacle, vf = vitellogenic follicle.

(Dean 1906; Figure 2). No oocytes or developing egg cases were present within either oviducal gland. Fifty-eight follicles were visible in the 2 ovaries and no corpora lutea were observed. Non-vitellogenic follicles ranged in diameter from 1 to 7 mm (mean = 3.65; sd = 1.96). Vitellogenic follicles ranged in diameter from 9 to 35 mm (mean = 17.58; sd. = 9.96) and appeared to be separable into 6 size cohorts (Figure 3). The follicle pair of greatest diameter were in the right ovary and consisted of 2 follicles with diameters of 35 and 32 mm. The next largest cohort was in the left ovary with follicle diameters of 26 and 25 mm. Cohort 3 was in the right ovary and consisted of a single 21 mm follicle. The remaining cohorts continued to show a pattern of decreasing diameters in alternating ovaries. To our knowledge, this is the first report of oocytes maturing in ovary-specific series for any chondrichthyan.

The presence of oocytes in various stages of development strongly suggests that *C. cubana* is reproductively active over a relatively protracted period and is consistent with the reproductive biology of other chimaeroids, such as *Callorhynchus callorhynchus* and *Hydrolagus coliei* (DiGiácomo and Raquel Perier 1994, Barnett et al. 2009). The absence of corpora lutea in the ovaries or egg case development in the oviducal glands or posterior oviducts suggests the specimen had not recently ovulated. Therefore, the number of vitellogenic follicles present in the ovaries indicates that the *C. cubana* we collected was capable of an annual fecundity of at least 12 young, assuming all vitellogenic oocytes eventually became fertilized, encased and deposited. In the absence of additional data on the reproductive biology of this species we must assume this is an estimate of maximum fecundity. It is likely, however, that the maximum annual fecundity is higher since vitellogenesis appears to be relatively rapid, as indicated by follicles of varying sizes and the simultaneous presence of vitellogenic and non-vitellogenic follicles.



**Figure 3.** Ovarian follicle diameter and oocyte cohort assignment as observed in an adult female *Chimaera cubana* collected south of St. Croix, U.S. Virgin Islands on 25 March 2009. All oocytes in cohort 7 were non-vitellogenic. □ = right ovarian follicle diameter, X = left ovarian follicle diameter.

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Growth Patterns of Shoal Grass *Halodule wrightii* and Manatee Grass *Syringodium filiforme* in the Western Gulf of Mexico

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## SHORT COMMUNICATION

# GROWTH PATTERNS OF SHOAL GRASS *HALODULE WRIGHTII* AND MANATEE GRASS *SYRINGODIUM FILIFORME* IN THE WESTERN GULF OF MEXICO

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## INTRODUCTION

Seagrass beds are a valuable resource because of the numerous roles they play in coastal systems. Seagrass blades provide habitat for abundant micro- and macro-algal communities, which in conjunction with the seagrass, contribute substantially to primary productivity in estuarine systems (Heck and Valentine 2006). The blades and roots stabilize sediments, which improves water clarity and increases light penetration, further increasing primary production (Zieman 1982, Gacia and Duarte 2001). Seagrass beds may also provide increased growth rates, critical habitat, and predation refuges for a variety of organisms (e.g., Irlandi and Peterson 1991, Hemminga and Duarte 2000) and have an increased abundance and diversity of juvenile and adult fish and other epibenthic organisms (Summerson and Peterson 1984, Heck et al. 1995).

In Texas, like most of the western Gulf of Mexico (GOM), shoal grass (*Halodule wrightii*), manatee grass (*Syringodium filiforme*), and turtle grass (*Thalassia testudinum*) are the most common seagrasses (Zieman 1982, Quammen and Onuf 1993, Withers 2002). Eighty percent of seagrass beds in Texas currently occur in the Laguna Madre (hereafter LM), a hypersaline lagoon that separates a coastal barrier island (Padre Island) from the Texas mainland (Pulich 1998, Tunnell and Judd 2002). Seagrasses were once common in many Texas bays, but have disappeared or declined in coverage in many areas due to anthropogenic causes (Pulich and Onuf 2007). Fortunately, the loss of seagrasses in Texas bays was offset by the increase in seagrass abundance in the LM due to the moderation of salinity after dredging of the Gulf Intracoastal Waterway (Quammen and Onuf 1993). Shoal grass can survive and grow in salinities from 5–80 (McMillan and Moseley 1967) and this seagrass dominated the LM for decades because of its ability to withstand these extreme salinities (Withers 2002).

Shoal grass harbors a diverse resident fauna (Tolan et al. 1997) and the migratory redhead duck (*Aythya americana*) population depends on shoal grass in the LM for food during the winter season (Cornelius 1977). Shoal and manatee grass are currently present in the upper LM, with shoal grass historically being dominant (Quammen and Onuf 1993) and extensively studied (e.g., Dunton 1994, 1996). However, manatee grass is increasing in coverage

in much of the LM and is steadily replacing shoal grass in this system (Quammen and Onuf 1993, Pulich and Onuf 2007). In other areas such as Corpus Christi Bay, shoal, manatee, and turtle grass have coexisted for the past 20 yrs (Czerny and Dunton 1995, K. Dunton pers. comm.).

Although manatee grass is becoming increasingly abundant in Texas bays, its growth characteristics have not been measured in the western GOM. Changes in seagrass species composition can have significant community effects (Micheli et al. 2008), but the effects of a transition from shoal to manatee grass in the LM have not been extensively studied (but see Tolan et al. 1997). The goals of our study were to measure growth patterns of these two seagrass species in two locations in the western GOM that vary in salinity, epiphyte loads, and nutrient inputs.

## MATERIALS AND METHODS

We selected two locations (bays) for this study: the East Flats section of Corpus Christi Bay (CCB) and another in the upper LM. Corpus Christi Bay is an urban estuary that receives substantial nutrient inputs, which are much higher than in the LM. Water exchange occurs more readily in CCB, giving this location lower, albeit more variable, salinity. By utilizing these locations, we were able to measure growth characteristics of shoal and manatee grass under different abiotic conditions. In both CCB and LM, we sampled monospecific stands of manatee grass that were adjacent to monospecific stands of shoal grass. Seagrass beds were separated by ~50 m in LM and ~500 m in CCB, and all were located in about 1.3 m of water (referenced to MLLW). GPS coordinates were 27°24.793'N, 97°21.224'W (shoal grass) and 27°24.805'N, 97°21.214'W (manatee grass) in the LM and 27°48.581'N, 97°07.323'W (shoal grass) and 27°48.758'N, 97°07.195'W (manatee grass) in CCB. We placed a PVC pole near the center of each seagrass bed and all growth characteristics were made within 10 m of these poles for each species.

Hydrolab minisondes were deployed in both locations and set to measure salinity and water temperature over a 60 s period daily for 10–14 d. We averaged the salinity and temperature for each 60 s measurement and then averaged these values for a grand mean of

temperature and salinity for each deployment period

We quantified epiphyte load on shoal and manatee grass in both locations in June 2007 when epiphytes were abundant, as epiphytes can strongly influence seagrass growth and mortality (Burd and Dunton 2001, Duarte 2002, Lirman and Cropper 2003). Our methods consisted of taking 5 randomly sampled, 10 cm diameter core samples using a polyvinyl chloride (PVC) corer (Johnson and Heck 2006) from each seagrass type. Within each core sample, 3 seagrass shoots were randomly selected for epiphyte quantification. The blade surface area was standardized by only using the oldest 10 cm of growth (top of the grass) with no obvious signs of grazing or other damage. We then carefully scraped off the epiphytes with a scalpel and transferred them to pre-weighed (0.001 g) Whatman GF/C filter paper. The filter paper and epiphytes were dried in a convection oven and weighed (0.001 g), and the total weight was subtracted from the original filter paper weight to quantify the epiphyte load. The epiphyte weight of the 3 blades was averaged to produce one epiphyte value per core sample. This produced 5 samples of epiphyte weight per location for both shoal and manatee grass.

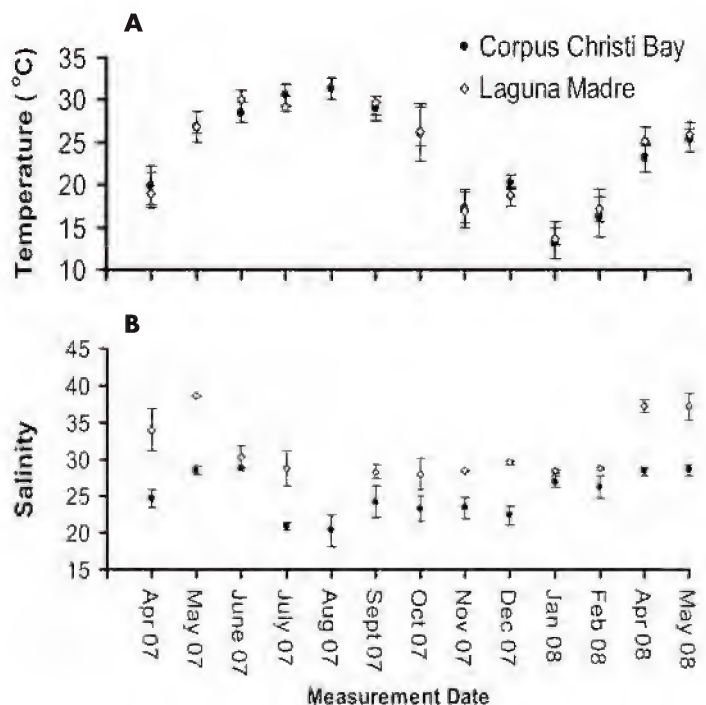
We sampled seagrass growth characteristics during consecutive peak growing seasons from March 2007 through June 2008. Sampling was conducted every 10–28 d ( $n = 27$  dates) depending on the season and weather conditions. We measured shoot density, root:shoot ratio (RSR), and primary growth rate in each location to determine the annual mean primary productivity patterns for each seagrass species. We also measured the density of reproductive shoots produced by manatee grass in each location. Daily variation in temperature and salinity are less likely to influence seagrass growth patterns than longer term differences (Dunton 1990, 1994), thus we pooled our data over date to focus specifically on comparing only seagrass growth patterns.

To measure primary growth, we used the clipping technique of Virnstein (1982); however, due to turbidity, we “harvested” the samples rather than photographing growth (Dunton 1990). This technique consisted of haphazardly selecting and trimming 0.25 m<sup>2</sup> plots ( $n = 3$ ) of shoal grass and 0.25 m<sup>2</sup> plots ( $n = 3$ ) of manatee grass in each location on each sampling date. Cuts were made 1.0 cm above the basal sheath for shoal grass, which allowed us to sample continuous growth (Dunton 1994). For manatee grass, cuts were made 6.0–7.0 cm above the basal sheath as preliminary results indicate that clipping below this height resulted in blade death. On each sampling date, a 10.0 cm diameter core sample, ~10.0 cm deep, was taken from each newly clipped plot as well as from each plot that had been clipped on the previous sampling date. Ten blades from the sample of the newly clipped plot were measured and averaged to determine the mean cut length at time 0 (i.e., mean blade length above substrate after clipping). The length of every blade was measured from the second core, which was taken 10–28 d after clipping. The mean cut length calculated im-

mediately after clipping was subtracted from the mean total length in the second core to determine the amount of growth in each of the 3 plots sampled. Growth rate (cm/d) was calculated by dividing the mean growth rate by the number of days between clipping and harvesting. The growth rates calculated for each core sample were averaged to calculate the grand mean growth rates for each grass by location and date.

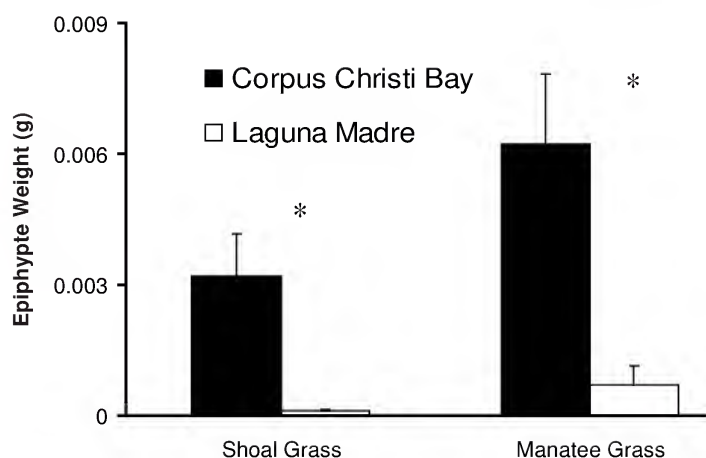
We also measured shoot density (#/m<sup>2</sup>) by collecting 78.5 cm<sup>2</sup> core samples ( $n = 3$ ) from an area outside our clipped plot, counting the shoots in each core, and multiplying by 127.4 to convert the value to m<sup>2</sup>. We pooled our density measurements from each core sample to calculate a mean density for each species by location and then averaged these mean density measures by date ( $n = 27$ ) to calculate a grand mean for shoal and manatee grass in each location.

To determine RSR, aboveground biomass (blades, g) and underground biomass (roots and rhizomes, g) were measured from shoal grass and manatee grass beds in each location during each sampling date ( $n = 27$ ). Three random core samples (78.5 cm<sup>2</sup>, 10.0 cm diameter) were taken to a depth of ~15.0 cm to ensure the collection of all root and rhizome structures. We haphazardly removed 10 blades from each core sample that had rhizomes attached, divided them into above and below ground sections, and scraped off any epiphytic material from the above ground portion. Above and below ground sections were dried separately in a convection oven at 60°C for 96 h and individually weighed from each



**Figure 1.** Monthly water quality measurements in each location (bay) during the study. A. Temperature (mean  $\pm$  sd). B. Salinity (mean  $\pm$  sd). The variability within each measurement period was low and using se resulted in the error bars being obscured by the data points.





**Figure 2.** Plot of epiphyte weight (g; mean + se) on shoal and manatee grass ( $n = 5$ ) from both locations (bays). \* - significant difference between locations.

core sample to calculate the RSR for each blade. Mean RSRs were calculated by species in each location by date ( $n = 27$ ). A grand mean RSR was calculated for each seagrass species in each bay by averaging the RSR values from all sampling dates.

We also counted the number of reproductive shoots in the RSR core samples collected in manatee grass beds on 6 sampling dates between March and May in 2007 and 5 sampling dates between March and May 2008. This was done because a high number of reproductive shoots may suggest lateral growth that would not be apparent from a 'clip and harvest' measurement. Shoal grass reproductive shoots were not observed during the study. As with shoot density, we multiplied the number of reproductive shoots by 127.4 to convert this value to number per  $m^2$ . Since we took 3 core samples on each sampling date, the number of reproductive shoots in each core sample was averaged.

#### Data analysis

We compared the grand mean of temperature and salinity between CCB and LM with a Student  $t$ -test (Sokal and Rohlf 1995). We then compared grand mean density, grand mean growth rates and grand mean RSR for each seagrass species between locations with a Student  $t$ -test (Sokal and Rohlf 1995). We compared the mean number of shoots pooled by date ( $n = 6$  in 2007 and  $n = 5$  in 2008) between locations by year with separate Mann-Whitney  $U$  tests because our data did not meet  $t$ -test assumptions (Sokal and Rohlf 1995).

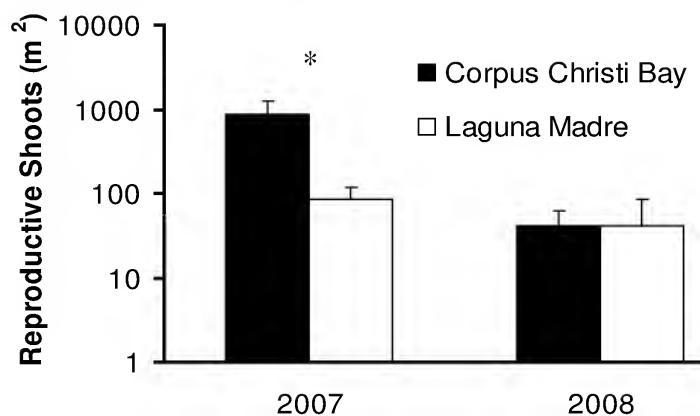
## RESULTS AND DISCUSSION

Temporal measurements of water temperature and salinity are presented in Figure 1 to illustrate seasonal trends. However, statistical analysis was performed only on the grand mean values ( $n = 13$ ) between locations. Water temperature ranged from  $13.7^{\circ}\text{C}$ – $29.9^{\circ}\text{C}$  and was not statistically different between the LM and CCB ( $t = 0.18$ ,  $p = 0.85$ , Figure 1A). Salinity was significantly higher in LM ( $t = 4.46$ ,  $p < 0.01$ , Figure 1B). The mean salinity in the

LM was 34.0 and ranged between 28.0–38.5 as compared to CCB with a mean salinity of 24.7 (range 20.3–28.8).

Epiphyte weight on shoal grass was significantly (32x) greater in CCB than in LM ( $t = 3.18$ ,  $p < 0.05$ ,  $n = 5$ , Figure 2). Similarly, the epiphyte weight recovered from manatee grass was significantly (9x) greater in CCB than in LM ( $t = 3.30$ ,  $p < 0.05$ ,  $n = 5$ , Figure 2). Previous research revealed that nutrient inputs are much greater in CCB than in LM (Quammen and Onuf 1993, Lee and Dunton 2000) and higher ambient nutrient levels are most likely responsible for the greater epiphyte weight measured in this study.

Shoal grass shoot density was significantly higher and more variable in the LM ( $t = 2.94$ ,  $p < 0.01$ , Table 1). Shoal grass shoot density peaked in LM in March 2008, reaching a density of  $\sim 7000$  shoots/ $m^2$ . In CCB, shoal grass density peaked at  $\sim 3600$  shoots/ $m^2$  in May of 2008. Shoot density was lowest in LM with  $\sim 470$  shoots/ $m^2$  in October 2007 and CCB had its lowest density of  $\sim 850$  shoots/ $m^2$  in November of 2007. Manatee grass shoot density was also greater and more variable in LM (Table 1). A  $t$ -test revealed statistical differences between the shoot densities of manatee grass between locations ( $t = 3.18$ ,  $p < 0.01$ , Table 1). The LM reached its peak density of  $\sim 4000$  shoots/ $m^2$  in May 2007 and CCB density peaked at  $\sim 2100$  shoots/ $m^2$  in June 2007. The lowest density observed was  $\sim 420$  shoots/ $m^2$  in CCB in October 2007 and  $\sim 540$  shoots/ $m^2$  in LM in November 2007.



**Figure 3.** Plot of number of reproductive shoots (mean + se) produced by manatee grass from March to May 2007 ( $n = 6$ ) and March to May 2008 ( $n = 5$ ) in Corpus Christi Bay and the Laguna Madre. \* - significant difference between locations.

Root:shoot ratios determine seasonal differences between the aboveground and belowground biomass fractions of seagrass, reflecting seagrass energy allocation (Dunton 1994, 1996). Higher ratios occur during the winter season when plants are dormant and are allocating more energy into roots and other below ground structures, but ratios decrease when energy is allocated toward above ground growth in the spring and summer. The RSR ratios ranged from 1.05–4.9 in shoal grass and 0.44–2.56 in manatee



**TABLE 1.** Grand mean growth characteristics  $\pm$  se (range of values in parentheses) of shoal and manatee grass in two Texas bays. Grand means were calculated from the means of 27 sampling events of monospecific stands of shoal grass and manatee grass in Corpus Christi Bay, TX and the Laguna Madre Texas. \* - significant difference between locations.

Growth Parameter	Shoal Grass		Manatee Grass	
	Corpus Christi Bay	Laguna Madre	Corpus Christi Bay	Laguna Madre
Shoot Density (number/m <sup>2</sup> )	2274 $\pm$ 439 (854–3605)	3347 $\pm$ 555 (471–6969)*	1254 $\pm$ 281(420–2128)	1774 $\pm$ (548–3965)*
Root:Shoot Ratio (RSR)	2.25 $\pm$ 0.37 (1.05–4.90)	2.13 $\pm$ 0.23 (1.08–4.2)	1.17 $\pm$ 0.19 (0.44–2.56)	1.28 $\pm$ 0.21 (0.49–2.13)
Growth Rate (cm/day)	0.41 $\pm$ 0.06 (0.07–0.80)*	0.27 $\pm$ 0.05 (0.07–0.87)	0.52 $\pm$ 0.14 (0.060–01.2)	0.41 $\pm$ 0.11 (0.04–1.1)

grass (Table 1). Ratios were not significantly different between CCB and LM for either shoal grass ( $t = 0.05$ ,  $p = 0.61$ , Table 1) or manatee grass ( $t = 0.93$ ,  $p = 0.35$ , Table 1).

Shoal grass grew significantly faster in CCB ( $t = 2.68$ ,  $p < 0.05$ , Table 1). Annual mean growth rates for shoal grass were 0.41 cm/d and 0.27 cm/d in CCB and LM, respectively. In both locations, the period of slowest growth occurred in January 2008 and was calculated in both at 0.07 cm/d. Shoal grass peak growth of 0.87 cm/d occurred in LM in September 2007, while growth peaked at 0.81 cm/d in CCB in July 2007.

Manatee grass grew faster in CCB with an annual mean rate of 0.52 cm/d as compared to 0.43 cm/d in LM, but these rates were not statistically different ( $t = 1.13$ ,  $p = 0.23$ , Table 1). Peak growth rate of 1.11 cm/d occurred in LM in June 2007, while the least growth of 0.05 cm/d occurred in March 2007. Peak growth rates of 1.20 cm/d occurred in CCB in August 2007, while the slowest growth in CCB was 0.06 cm/d in January 2008.

Shoal grass reproductive shoots were not observed during the study. Manatee grass produced a significantly higher number of reproductive shoots in LM ( $\sim 875$  reproductive shoots/m<sup>2</sup>) as compared to CCB ( $\sim 85$  reproductive shoots/m<sup>2</sup>,  $z = 2.16$ ,  $p < 0.05$ , Figure 3) from March to May 2007. Numbers of reproductive shoots were not significantly different from March to May 2008 ( $z = 0.63$ ,  $p = 0.73$ , Figure 4) with  $\sim 41$  shoots/m<sup>2</sup> at both locations.

Because manatee grass has historically been much less common than other seagrasses in Texas (Quammen and Onuf 1993), its seasonal growth patterns in the field have not been carefully studied in this region. Our study provides the first documentation of manatee grass growth and energy allocation patterns in the western GOM. Our estimates of shoal grass growth and RSR ratios are consistent with earlier measurements made by Dunton (1990, 1994, 1996), suggesting that our technique provided an appro-

priate assessment of primary production of both species.

Our study locations are exhibiting different patterns of seagrass succession. Seagrass succession in the LM is following the traditional model proposed by Zieman (1982) where shoal grass, the pioneer species, is replaced by manatee grass and finally by turtle grass, the climax community (Quammen and Onuf 1993, Pulich and Onuf 2007). In contrast, all three seagrasses have coexisted for the past 20 yr in CCB without an obvious loss in overall coverage of any one species (Czerny and Dunton 1995, K. Dunton pers. comm.).

Fluctuations in salinity can be stressful to seagrasses and slow or stop succession so that multiple species coexist (Montague and Ley 1993). Salinity fluctuations in CCB, coupled with higher epiphyte loads, may act like moderate disturbances, thus stalling seagrass succession and promoting coexistence of these species. Conversely, the more constant salinity levels and lower epiphyte loads in LM are allowing succession to proceed with manatee grass slowly replacing shoal grass. Both seagrasses grew faster in CCB and had higher epiphyte loads, which were likely caused by greater nutrient inputs at this location.

We observed higher shoot density in both seagrasses as well as greater energy allocation to lateral growth and reproductive structures by manatee grass in LM, suggesting that conditions in this location are more favorable for seagrasses than in CCB. Should seagrass succession proceed in LM, a significant change in species composition in this important and unique ecosystem will likely occur. We must continue to monitor changes in seagrass composition in Texas to better understand potential consequences of species replacement. Since seagrass composition strongly influences community structure (Tolan et al. 1997, Micheli et al. 2008), it is necessary to understand the mechanisms driving seagrass change especially with the current decline in seagrasses worldwide. This study provides important baseline information to begin this process.

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Obituaries - Rezneat Milton Darnell, Jr. (1924-2009) and Royal Dallas Sutkus (1920-2009)

Molly Marie Darnell

Henry L. Bart Jr.

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## OBITUARY

### REZNEAT MILTON DARNELL, JR.

Rezneat Milton Darnell, Jr., well-known and respected ecologist and marine biologist, died on 22 December, 2009 in



*Rez Darnell working on his book in his office at home, spring 2005.*

Minneapolis, MN after a brief illness with pneumonia and suspected lung cancer.

Rez was born in Memphis, TN on 14 October, 1924. His parents were Rezneat

Milton Darnell, Sr. and Matilda Millen Darnell.

Dr Darnell was Professor of Oceanography at Texas A&M University from 1968 until his retirement in 1995 as Professor Emeritus.

Darnell graduated from Southwestern College (now known as Rhodes College) in Memphis, TN with a Bachelor's degree in Zoology in 1946. He received his Master's degree in Biology & Genetics from Rice University in Houston in 1948 and his Ph.D. in Ecology from the University of Minnesota in 1953. Before coming to Texas A&M, Darnell served three years as Instructor at Tulane University in New Orleans, LA and 13 years as Assistant Professor at Marquette University in Milwaukee, WI.

Dr. Darnell published numerous scientific papers on the ecology of the Gulf of Mexico. His last work, *The American Sea: A Natural History of the Gulf of Mexico*, soon to be published by the Texas A&M Press, is a comprehensive book on the ecology of the Gulf of Mexico and is eagerly awaited by colleagues across the nation. His many graduate students have praised his lectures and his ability to clearly and concisely explain the complex environmental problems of our planet.

Dr. Linda Pequegnat, former Research Scientist in the Oceanography Department at Texas A&M and a friend and colleague of Dr. Darnell's says, "Rez has been called 'The Great Synthesizer' because of his ability to take detached scientific information and organize it into meaningful overviews that explain the 'big picture' of ecological relationships in the natural world. He was also a 'Renaissance Man' with extensive knowledge and experiences in such diverse areas as music, languages, and history – in addition to his vast scientific knowledge. His forthcoming book, soon to be published by the Texas A&M Press, on the history, biology, ecology, and management of the Gulf of Mexico pulls together more information about the Gulf of Mexico than has ever before been amassed in one Volume."

Dr. Darnell was preceded in death by his parents and by his older brother, Rowland Jones Darnell. He is survived by his loving and caregiver daughter, Molly Marie Darnell of Minneapolis, MN, his brother J. Millen Darnell of Memphis, TN, his first wife Jeanne Hellberg Darnell of Minneapolis, MN, and many nieces and nephews including James Darnell, serving his second tour of duty in Afghanistan.

– Molly Marie Darnell

### ROYAL DALLAS SUTTKUS

Royal D. Suttikus, or "Sut", as he was affectionately known to family and friends, holds a special place in southeastern ichthyology, having described a significant component of the region's ichthyofauna. On 5 January, 2010, the ichthyological and broader biological communities were awakened to the news that Royal D. Suttikus had passed away one week earlier (28 December 2009) surrounded by family in Decatur, Georgia, less than six months shy of his 90 birthday. Over a professional career spanning 65 years, he established a legacy that will serve the biological communities for many years to come. His great skill and his insatiable appetite for field collecting are legendary. The collections he amassed—primarily fishes, but also important regional collections of plants, aquatic invertebrates, amphibians and reptiles, and mammals—constitute one of the most comprehensive, long-term records of biotic change in existence. The following account of his remarkable life is excerpted from an article currently

*Royal D. Suttikus from the fall of 2000 in the fish collection that would soon be named in his honor.*

in press in the journal *Copeia*.

Suttikus was born 11 May 1920 in Ballville, Ohio, the third of four children of John Albright Suttikus and Myna Louise Schultz Suttikus. Royal, as he was called as a boy, developed a love for natural history in early childhood. He hunted rabbits and pheasant with brother Merlin, and enjoyed birding, gathering wildflowers and collecting insects. He taught his friends about horned worms and hawk moths. He fished with his father below the hydrodam on the Sandusky River, catching white and black crappie. He caught small fish with his hands while searching for crayfish among slabs of rock. He recalls seeing redhorse



suckers spawning along the Sandusky River and shooting an Egyptian goose with a bow and arrow along the Grand River in Michigan. He read Darwin's *On the Origin of Species* while in high school.

Suttkus graduated from Fremont Ross High School in 1937 then worked in a celery garden for 2 years at a salary of \$0.25 cents per hour to earn money for college. In the fall of 1939, he enrolled in Michigan State University, eventually majoring in Wildlife Management.

Suttkus joined the R.O.T.C. at Michigan State, where he trained in field artillery. After earning his bachelor's degree, he enrolled in Officer's Commission School. When he finished his training, he was promoted to Second Lieutenant and attached to the 686th Field Artillery, an all African American battalion. His battalion went to South Wales in 1944 then crossed the English Channel to France, where his training was put to immediate use in the Battle of the Bulge.

After his discharge from the Army in June 1946, he was accepted to the graduate program in the School of Agriculture at Cornell University, where he studied under Edward Raney. He met his bride to be, Jeanne Elizabeth Robinson, while working for New York Fish and Game on Saranac Lake. They were married in December 1947. Son, Jayson, the first of three children, was born in Ithaca, NY, two years later in January 1949.

Suttkus accepted a faculty position in Zoology at Tulane University in the fall of 1950. Daughter, Ramona, was born in New Orleans in April 1951; daughter, Jan, was born in September 1954. Suttkus devoted his career at Tulane to collection building and studies of the taxonomy and natural history of specimens he collected. From 1963 to 1968, he was Principal Investigator of the NIH-funded, Environmental Biology Training Program, a summer program in which students received lectures and training while in the field collecting and preparing specimens of plants, invertebrates, fishes, amphibians, reptiles, birds, mammals, and fossils. Additionally, he directed 24 graduate students during his career at Tulane University (10 M.S., 14 Ph.D.).

In 1963, Suttkus started a consulting business with his long-time Tulane colleague, the late Gerald E. Gunning. Their first contract was a survey of ten stations on the Pearl River near Bogalusa, Louisiana for a pulp and paper mill. The survey started with monthly samples in April

1963, then switched to quarterly (seasonal) collections a year later. A quarterly survey of eight stations on the upper Pearl River was initiated in 1973. Suttkus continued both surveys until 2005. A survey of the lower Alabama River started in 1969 and continued until 2000. A survey of the Red River near Alexandria, LA was established in 1976 and ended in 2002. Shorter-term surveys were conducted on the Perdido Bay System, Sabine River, Mississippi River and Calcasieu River. All of the collecting on these surveys was supervised by Suttkus and involved standardized gear, technique and environmental sampling. Suttkus also collected marine organisms during oceanic cruises in the Gulf of Mexico, Indian Ocean, off the coasts of Peru and Venezuela, and around the Galapagos Islands. All of the specimens collected (fishes and any amphibians, reptiles, mussels, and decapods that happened to be collected) were preserved and ultimately cataloged into Tulane's natural history collections.

Suttkus published 125 papers during his career, including 54 of which deal directly with fish taxonomy and systematics, 41 on various aspects of fish life history and/or distribution, and 27 reports based on his fish monitoring surveys. As a sign of his taxonomic breadth, 11 of his papers deal with mammals, three deal with crayfishes, and one deals with freshwater mussels. Among his systematic and taxonomic contributions are descriptions of 35 new fish species, 29 of which are freshwater species largely confined to the southeastern United States.

Suttkus's greatest contributions to southeastern biology were his collections. He built the Tulane fish collection on a foundation of just two mounted fish specimens left over from an early exhibit museum. By 1968, the fish collection had grown to a size of just over two million specimens, overfilling its space on the main Tulane campus. Later that year, the fish collection, along with birds, mammals and vertebrate fossil collections left over from the early exhibit museum, plus the thousands of specimens of plants, amphibians, reptiles, mammals and fossils amassed by Suttkus and students in the Environmental Biology Training Program, were moved to a 500 acre parcel of land on the Mississippi River

near Belle Chasse, LA, which Tulane had acquired from the U.S. Navy. The land, which had served as an ammunition storage depot during WWII, eventually became the F. Edward Hebert "Riverside" Research Laboratories. The collections became part of what was initially called the Systematics and Environmental Biology Laboratory. In 1976, Suttkus convinced the Tulane administration to formally recognize the collections at Riverside as the Tulane University Museum of Natural History, and to appoint him as the Museum's first Director.

Suttkus officially retired from Tulane University in 1990. In fall 2000, a jubilee celebration was held in New Orleans to honor Suttkus's 50 years of service to Tulane University and his contributions to southeastern biology. At a special closing ceremony held under a tent beside the fish collection, the Dean of Arts and Sciences read a proclamation from the President, Faculty and Administrators of Tulane University, officially renaming the Tulane Fish Collection, the Royal D. Suttkus Fish Collection, and granting Suttkus the title of Emeritus Curator of Fishes.

Suttkus continued collecting and depositing specimens in the fish collection until just before Hurricane Katrina devastated the Gulf Coast in August 2005. Suttkus's home near the beach in Ocean Springs, Mississippi was flooded and badly damaged by the high winds and storm surge that accompanied the hurricane. He lost nearly all of his possessions, including his field notes and most of his library. What little remains of his library is now part of the Royal D. Suttkus Fish Collection.

Since the hurricane, Suttkus and Jeanne had been living in an apartment in Atlanta, where he continued to publish his research. Suttkus had also been battling prostate cancer. His health took a downward turn in early December 2009. However, family members say that his mind was clear and his spirits were high until shortly before he died. He is survived by his wife Jeanne, son Jayson, daughters Ramona and Jan and their families, brother Hazen and numerous extended family members.

– Henry L. Bart, Jr.